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The effects of ad libitum and restricted feeding on Yorkshire pigs selected for reduced residual feed intake

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by

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ABSTRACT

Residual feed intake (RFI), defined as the differences between observed and expected feed intake based on growth and backfat, has been used to select for improved feed efficiency in beef cattle, poultry, and now swine. However, little is known about the main biological factors that contribute to the variation in RFI in swine. The objectives of the experiments in this thesis were to compare the 5th generation of a line of pigs selected for reduced RFI (Select) against a randomly selected control (Control) line for performance parameters and to examine the biological contribution of visceral mass, carcass and chemical carcass composition, and predicted maintenance requirements on the overall efficiency during two stages of growth: the early post-weaning period (EGP) and late growth period (LGP) prior to market weight. In both experiments, Select and Control line pigs were paired based on age (~65 and 132 d for EGP and LGP, respectively) and weight (23.9±4.2 and 74.8±9.9 kg, respectively) and the pairs were randomly assigned to one of four feeding level treatments: 1) ad libitum (Ad); 2) 75% of Ad (Ad75); 3) 55% of Ad (Ad55); and 4) weight stasis to maintain a constant body weight (WS). In both experiments (EGP and LGP), pigs were individually penned and on feed treatment for 6 weeks. Overall, under Ad feeding, the Select line consumed 8 to 10% ($p < 0.09$) less feed compared to the Control, with no significant difference in weekly BW ($p < 0.80$). In general, the Select line under the Ad treatment had less backfat and carcass fat % but no other significant differences in carcass chemical composition. Under restricted feeding, the Select line had an increase in BW ($p = 0.10$) while consuming the same amount of feed as the Control, in both experiments. Furthermore, no significant differences in carcass chemical composition were found. The Select line had

lower visceral weights but this was only significant ($p < 0.01$) for the LGP experiment. In the EGP experiment, the WS treatment showed no significant differences in feed intake or BW between the Select and Control line. Conversely, for the LGP experiment, the Select line required less feed than the Control by the end of the experiment to maintain static BW ($p < 0.08$). Furthermore, there was a trend for the Select line to have reduced maintenance energy requirements ($p < 0.13$) for the LGP experiment, as estimated by regression of consumed on retained energy. In conclusion, selection for reduced RFI has reduced feed intake, with no significant differences in growth performance but reduced backfat, reduced carcass fat%, and lower maintenance requirements. The results of this thesis show that carcass composition and energy partitioning, primarily differences in carcass fat%, and reduced estimated maintenance requirements may significantly contributed to the differences in RFI.

CHAPTER 1. GENERAL INTRODUCTION

Introduction

Feed efficiency is a key component to the success, profitability and sustainability of swine production. Feed efficiency has traditionally been calculated from the ratios of gain:feed or feed:gain. However, there is a measurement of feed efficiency that is unrelated to important production traits such as growth and backfat. This is called residual feed intake (RFI). Residual feed intake is calculated as the observed feed intake minus the expected feed intake given a certain level of growth and backfat (Koch et al., 1963). In a given population, a proportion of the animals will consume more feed than is required for maintenance, growth, and backfat, while some animals will consume less. These differences between the expected and observed feed intake is the residual aspect of RFI. Animals that consume less feed than expected have low residual feed intake, which makes them more feed efficient and desirable. Animals that consume feed above their expected level of feed intake for a given amount of backfat and growth, have a high RFI value and are therefore classified as less efficient.

Geneticist have strived, and succeeded, to increase feed efficiency in swine through genetic selection and breeding for average daily gain and backfat (Cleveland et al., 1982; Kuhlers and Jungst, 1983; Woltmann et al., 1992). Because a substantial proportion of differences in feed intake and efficiency are unrelated to growth and backfat (i.e. residual feed intake), geneticists have successfully increased feed efficiency by decreasing feed intake without major alteration to growth rate and slight differences in backfat (Cai et al., 2008; de Haer et al., 1993; Gilbert et al., 2007; Johnson et al., 1999). However, collection of feed intake data is tedious and expensive. Therefore, cheaper and faster methods need to be developed to better aid in selection for increased feed efficiency. In order to accomplish this challenging task, the molecular and physiological characteristics that underlie feed efficiency need to be identified in agriculturally important animal species.

The concept of residual feed intake was introduced in beef cattle in the early 1960’s (Koch et al., 1963). However, this concept is relatively new to the swine industry, as it was not developed until approximately 20 years later (Foster et al., 1983). Some of the main biological factors that contribute to the variation in residual feed intake have been quantified in beef cattle (Herd and Arthur, 2008; Richardson and Herd, 2004a) and poultry (Luiting et al., 1991). To this extent, the contribution of different physiological mechanisms to the variation in residual feed intake in swine is largely unknown.

In beef cattle, the main biological factors that contribute to RFI variation are physical activity, feeding behavior, body composition, digestibility, heat increment of fermentation, protein turnover and tissue metabolism, and stress (Herd and Arthur, 2008). This information provides a good basis for the swine industry to establish species specific biological factors that contribute to RFI variation, as many of the factors may, in fact, be similar. However, some of these factors in beef cattle (i.e. heat increment of fermentation) may not be fully applicable to swine due to the differences in anatomy. Therefore, it is critical to define the factors that contribute to RFI in pigs. With this knowledge, easy measureable traits could be developed to rapidly and feasibly select for reduced RFI and high efficient pigs.

In 2001, using purebred Yorkshire pigs, a selection line for reduced residual feed intake, along with a randomly selected control line was begun under the direction of Dr. Jack C. M. Dekkers. These lines were developed to look at direct and correlated response to selection, estimate genetic parameters, understand the biological mechanisms behind residual feed intake and feed efficiency, and look at differences in gene expression. Through these objectives, these lines have become the main source of a collaborative effort between geneticists, molecular biologists, nutritionists and behaviorists, particularly to examine the main biological factors that contribute to RFI. This thesis will focus on the main biological factors of performance traits, carcass composition, and estimated maintenance requirements. The objectives of this thesis were:

1. To evaluate Yorkshire barrows from the 5th generation of a low residual feed intake line against a 5th generation, randomly selected control line, for performance under ad libitum and restricted feeding at two different stages of growth.
2. To evaluate the contribution toward the variation in RFI of backfat, loin eye area, carcass composition, and carcass chemical composition between the two lines under ad libitum and restricted feeding.
3. To evaluate the estimated crude maintenance requirements between the two lines of pigs under a weight stasis treatment designed to maintain body weight throughout the test at two different stages in the growth phase.

Thesis Organization

Based on the work to achieve the objectives of this dissertation, two manuscripts were written for submission to scientific journals and are included as chapters in the thesis. A review of literature as background for this research is in Chapter 2. Evaluation of growth performance and carcass characteristics of young, post weaned pigs is described in Chapter 3 and the evaluation of growth performance and carcass characteristics of pigs nearing market weight is described in Chapter 4. Chapter 5 includes general conclusions and an overall discussion of the research.

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CHAPTER 2. LITERATURE REVIEW

Measures and importance of feed efficiency

Feed efficiency (FE) is an integral part of profitability in swine production, as the cost of feed can account for 75% of the variable costs associated with production. Improving FE in the terminal production setting leads to increased profits for producers. However, feed efficiency is difficult to quantify as there is no one single trait that can be measured to calculate FE. Instead, FE is generally a function of an animal's feed intake and growth rate. Traditionally, FE has been calculated as the ratio of feed:gain (feed conversion ratio) or its inverse, gain:feed (FE). The problem with selection based on these ratios is the assumption that the gain:feed ratio, or its inverse, responds as a single trait instead of the reality that two traits are acting upon the "single trait" (Gunsett, 1986). Feed intake is phenotypically positively correlated with other important economic traits such as growth rate (0.72 to 0.88) and backfat (0.49 to 0.64) (Cai et al., 2008; Hoque et al., 2009; Johnson et al., 1999).

Residual feed intake as a unique measure of feed efficiency

Approximately 36 to 64% of the variation in feed intake (FI) is related to production traits, such as growth rate and backfat (Luiting, 1990), which leaves a significant proportion of the variation in FI unaccounted. This unaccounted variation is referred to as residual feed intake (RFI). Residual feed intake is computed a number of different ways by adjusting for National Research Council requirements, or statistically adjusting for average daily gain (ADG) (Hoque et al., 2009; Johnson et al., 1999); ADG and backfat (BF) (Cai et al., 2008; Gilbert et al., 2007; Hoque et al., 2009); ADG, loin muscle content, and metabolic body weight (Gilbert et al., 2007); ADG and loin eye area (LEA) or ADG, BF, and LEA (Hoque et al., 2009). Thus, given the adjustments of ADG and BF, by definition, RFI is phenotypically unrelated to the production traits of growth and backfat. Residual feed intake was first suggested by Koch et al. (1963) to quantify feed efficiency in cattle. The deviation of the observed FI from the predicted FI is the residual in RFI and the desirable animals are those that have a negative deviation or low RFI (increased efficiency). In other words, animals that consume less feed than expected have low residual feed intake, which makes them more feed efficient for a given amount of lean gain. In swine, RFI has been shown to be moderately heritable, with estimates ranging from 0.15 to 0.38 (Cai et al., 2008; Gilbert et al., 2007; Hoque et al., 2009; Nguyen et al., 2005).

In beef cattle, two lines divergently selected for high and low RFI for 5 years resulted in an 11% decrease in FI with no difference in yearling weight (Herd et al., 2003). Similar results, with regards to a reduction in FI, were also found in divergent lines of laying fowl selected for residual feed intake for 15 and 18 generation for males and females, respectively (Bordas and Minvielle, 1999). In swine, pigs selected for low RFI after 4 generations consumed 165 g/d less feed compared to a randomly selected control line with a difference of 96 g/d in RFI; however, the low RFI line had 33g/d lower average daily gain (ADG) and 1.99 mm less backfat (Cai et al., 2008). Gilbert et al. (2006) reported a negative genetic correlation between RFI and ADG ($r = -0.16$) and RFI and BF ($r = -0.15$), and a positive genetic correlation between RFI and daily feed intake ($r = 0.38$). Many selection experiments have been conducted to determine selection response and genetic parameters for residual feed intake in swine; however, little is known about the biological factors that contribute to the increased feed efficiency of pigs selected for low RFI. Therefore, further research is needed to determine the underlying mechanisms of RFI to better aid selection for FE.

Biological factors that contribute to residual feed intake

Key biological factors that contribute to the variation in RFI have been quantified in beef cattle (Herd and Arthur, 2008; Richardson and Herd, 2004a) and poultry (Luiting et al., 1991). Biological factors that contribute to the variation in residual feed intake include protein turnover and tissue metabolism, stress, digestibility, physical activity, feeding behavior, and body composition. In beef cattle, these factors, along with heat increment of fermentation, account for 75% of the variation in RFI (Figure 2.1) (Richardson and Herd, 2004a). The main biological factors that contribute to variation in RFI have not been quantified in swine. However, many of the genetic parameters and production traits that are affected by response to selection in beef cattle and poultry are similar in swine. Therefore, many of the biological factors that contribute to the variation may be the same across species but in different proportions.

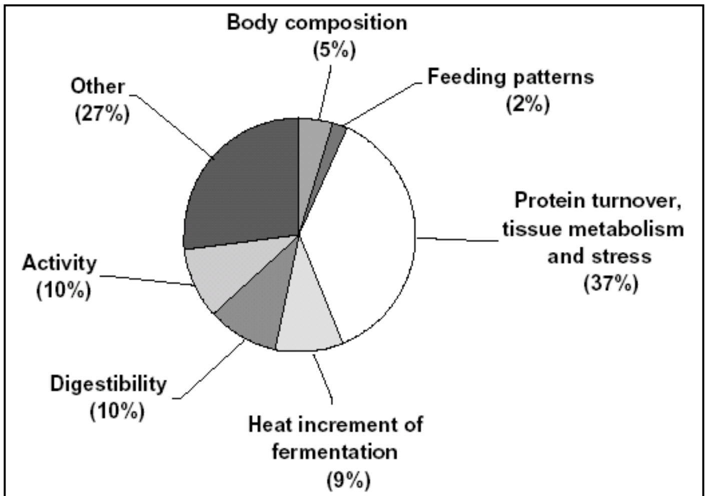

Figure 1. Contributions of biological mechanisms to variation in residual feed intake as determined from experiments on divergently selected cattle. Richardson and Herd, (2004)

<u>*Behavior.*</u> In beef cattle, feeding behavior accounted for 2% of the variation in RFI (Richardson and Herd, 2004a). In studies of beef cattle where RFI was estimated for individual animals but not divergently selected for RFI, feeding time per day, feeder visits

per day, and eating rate were all positively correlated with RFI (Lancaster et al., 2009b; Nkrumah et al., 2006; Robinson and Oddy, 2004). In swine, RFI has been found to be positively correlated with feeding time per day (min/d), and weak to no correlations were reported with feeder visits per day and eating rate (g/min) (Rauw et al., 2006; Von Felde et al., 1996). De Haer et al. (1993) reported similar correlations, except for the correlation between RFI and number of visits, which they found to be strong positive. Although the factors that contribute to the variation in RFI have not been fully quantified in pigs, the low correlations between RFI and feeding behavior traits suggests that feeding behavior may contribute little to the variation in RFI.

Physical Activity. Richardson and Herd (2004) found physical activity to be positively correlated (0.32) with RFI in beef cattle and for it to account for approximately 10% of the variation. Selection for food intake adjusted for body weight can indirectly reduce physical activity, as they are positively correlated (Moruppa, 1990). In lines of mice, animals selected for low heat loss (increased feed efficiency) were half as active compared to their high heat loss counterparts, which accounted for approximately 36% of the difference in feed intake as measured by regression of feed intake on log base 2 activity (Mousel et al., 2001). In chickens divergently selected for RFI, low RFI chickens had decreased physical activity, such as food pecking activity (Bordas et al., 1992; Braastad and Katle, 1989).

Pigs are curious and socially active animals, which would lead one to believe that social and locomotor activity contributes significantly towards the variation in RFI. To our knowledge, no published literature has examined the relationship between RFI and non-feeding, physical activity. Therefore, studies need to be conducted to investigate the extent to which physical activity contributes to the variation in RFI.

Digestion. In beef cattle, digestion accounts for approximately 10% of the variation in RFI (Richardson and Herd, 2004a). Feed that is not digested is excreted in the feces and results in lowered efficiency of feed utilization for important processes such as lean tissue deposition etc. In cattle divergently selected for high or low RFI, fecal pH and dry matter content were genetically negatively associated with RFI (Channon et al., 2004). However, these results must be viewed with caution as fecal pH is only a good indicator of starch fermentation (digested) (DeGregorio et al., 1982). Conversely, de Haer et al. (1993) found that digestibility did not contribute to the variation in RFI in pigs. These dissimilar findings may largely be due to differences in digestive systems between ruminants and monogastrics. However, further research needs to be performed in this area before completely ruling out digestion accounting for the variation in RFI in pigs.

Maintenance Requirements. Reduced maintenance energy requirements, defined as the energy cost of physiological functions (Van Milgen, 2006), could also contribute significantly to low RFI. Although visceral mass is comparatively small to muscle mass in the body, visceral tissue is very energetically expensive to maintain and function compared to muscle mass (Van Milgen et al., 1998). Noblet et al. (1999) examined the effects of sex and breed on maintenance requirements. When describing metabolizable energy intake as a function of muscle mass and visceral mass, while accounting for breed effects, visceral tissue contributed three times more to maintenance than muscle (Noblet et al., 1999). Furthermore, *ad libitum* fed pigs that consumed more feed had larger intestinal tracts and liver weights compared to pigs fed *ad libitum* that consumed less feed (Wiseman et al., 2007). Since RFI is positively correlated with feed intake (Cai et al., 2008), collectively these findings suggest that pigs selected for low RFI are expected to have smaller intestinal tracts and ultimately lower maintenance requirements. In beef cattle, selection for low RFI resulted in lower maintenance requirements, as estimated by the difference between total metabolizable energy intake and metabolizable energy required for growth (Herd and Bishop, 2000). Furthermore, Castro Bulle et al. (2007) reported a positive correlation between maintenance requirements and RFI (r = 0.42) in beef cattle selected for high growth and compared to a line with no selection. Luiting et al. (1991), reported that laying hens with lower RFI had lower basal metabolic rate and produced less body heat than hens with high RFI. Furthermore, Van Eerden et al. (2006) found that pullets with high RFI had more rapid energy metabolism and put more total energy into maintenance.

Carcass Composition. With the onset of the human obesity pandemic, dietitians have pushed for reduced fat consumption in the United States. This has had a large impact on meat animal agriculture. Through genetics, breeders have successfully transformed fat hogs from the 1960’s into lean, muscular animals due to the demand of consumers. However, selection for lean growth can have negative effects on meat quality such as intramuscular fat (Cameron, 1990; de Vries et al., 1994). By definition, RFI is unrelated to the production trait of BF at a phenotypic level (i.e. phenotypic correlation of 0); however, depending on the population, the genetic correlation between RFI and BF can be positive (Gilbert et al., 2007; Hoque et al., 2009) or negative (Cai et al., 2008; Nguyen et al., 2005). Furthermore, RFI was found to have a positive genetic correlation with intramuscular fat (r = 0.40) (Cai et al., 2008). In beef cattle with estimates of RFI, but not selection for RFI, Lancaster et al. (2009a) reported a positive genetic correlation between BF and RFI in Brangus heifers. Furthermore, Richardson et al. (2001) found that beef cattle selected for low RFI had significantly greater gain in protein throughout the 140 d test period and significantly less carcass fat, which included intramuscular and subcutaneous fat. At the metabolic level, increased fatness in cattle results in an increased concentration of serum leptin (Geary et al., 2003), which is positively correlated with steer RFI (Herd and Arthur, 2008). Therefore, body composition may explain some of the variation in RFI in swine; however, alterations in body composition can impact meat quality. Divergent selection for RFI in pigs resulted in a decrease in meat quality, as low RFI pigs had lighter meat color, which is driven by the lower ultimate pH of the low RFI pigs due to decreased oxidative capacity of skeletal muscle (Gilbert et al., 2007). Reduced ultimate pH results in reduced water holding capacity and unappealing appearance of meat to the consumer.

Selection for increased leanness is accompanied by increased body protein content, primarily in the form of muscle or lean accretion. Protein turnover, along with tissue metabolism, as measured by red and white blood cell parameters, accounted for approximately 37% of the variation in RFI in beef cattle (Herd and Arthur, 2008). Beef cattle divergently selected for RFI have shown that protein turnover is energetically expensive and differences in protein metabolism were observed. Additionally this translated into low RFI cattle having increased body chemical protein as a percentage of live weight at slaughter and decreased plasma protein (Richardson and Herd, 2004a). A reduction in protein turnover is desirable to increase feed efficiency, as decreased protein turnover would result in less energy used during the process.

Conclusions

The main biological factors that contribute to the variation in RFI are far more understood in beef cattle and poultry than in swine. Hence there is a great need to further understand the main biological factors that contribute to the variation in residual feed intake to improve lean gain efficiencies in pigs. However, this must not be at the expense of product quality. Many of the genetic parameters of RFI found in beef cattle and poultry are similar to those found in pigs. This provides a baseline for swine researchers to begin the process for better understanding RFI and FE. Selection for RFI requires collection of feed intake data, which is laborious and expensive, and ultimately not practical in the production setting. By understanding the biological factors that contribute to variation in RFI, and FE in general, less laborious and inexpensive selection criterion, such as an indicator trait, could be utilized in the production setting to increase FE.

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CHAPTER 3. EFFECTS OF AD LIBITUM AND RESTRICTED FEEDING ON EARLY PRODUCTION PERFORMANCE AND BODY COMPOSITION OF YORKSHIRE PIGS SELECTED FOR REDUCED RESIDUAL FEED INTAKE[1]

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Abstract

Residual feed intake (RFI), defined as the difference between observed and expected feed intake based on growth and backfat, has been used to select for improved feed efficiency in cattle, poultry, and pigs. However, little is known about the biological basis of differences in RFI in pigs. To this end, the objective of this study was to evaluate the 5th generation of a line of pigs selected for reduced RFI against a randomly selected control line for performance, carcass and chemical carcass composition, and overall efficiency. Here, emphasis was on the early post-weaning growth phase. One hundred barrows, 50 from each line, were paired by age and weight (22.6 ± 3.9 kg) and randomly assigned to 1 of 4 feeding treatments in 11 replicates: ad libitum (Ad), 75% of Ad (Ad75), 55% of Ad (Ad55), and

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weight stasis (WS), which involved weekly adjustments in intake to keep body weight (BW) constant for each pig. Pigs were individually penned (group housing was used for selection) and on treatment for 6 weeks. Initial BW did not significantly differ between the lines ($p < 0.17$). Under ad libitum feeding, the low RFI pigs consumed 8% less feed compared to control line pigs ($p < 0.10$), had less carcass fat ($p < 0.03$), but with no significant difference in growth rate ($p < 0.94$). Under restricted feeding, low RFI pigs under the Ad75 treatment had a greater rate of gain while consuming the same amount of feed as control pigs. Similarly, loin eye area tended to be larger for low RFI pigs under the Ad75 treatment ($p < 0.10$). Despite the greater gain, no significant line differences in carcass composition or carcass traits were observed. For the WS treatment, low RFI pigs had similar in BW ($p < 0.14$) while consuming slightly less feed (3.5%, $p < 0.34$) compared to control pigs, with no significant difference in carcass chemical composition, indicating the possibility that maintenance requirements may be lower for the low RFI line. Overall, selection for reduced RFI has decreased feed intake, with limited differences in growth rate but reduced carcass fat, as seen under ad libitum feeding. Collectively, the effects of selection for low RFI were observable even shortly after weaning, which allows for greater savings to the producer.

Introduction

Residual feed intake (RFI) is a unique measure of feed efficiency that accounts for differences in growth and backfat. RFI is calculated as observed minus expected feed intake for the pig’s achieved rate of gain and backfat (Kennedy et al., 1993; Koch et al., 1963; Luiting, 1990). In swine, RFI has been shown to be moderately heritable, with estimates ranging from 0.15 to 0.38 (Cai et al., 2008; Gilbert et al., 2007; Hoque et al., 2009; Nguyen et al., 2005). To investigate the genetic and biological basis of RFI, a selection experiment for reduced RFI (i.e., improved feed efficiency) in group-housed purebred Yorkshire pigs was undertaken at Iowa State University. After four generations, selection responses were evaluated by Cai et al. (2008) under group pen and ad libitum feeding conditions; gilts from the low RFI line consumed substantially less feed (165 g/d) but also had a slightly lower growth rate (33 g/d) and backfat (1.99 mm) relative to gilts from the randomly selected control. When adjusting for differences in growth and backfat, the difference in RFI was 96 g/d. Bunter et al. (2010) recently reported IGF-I to be positively genetically correlated with RFI, using the same population as Cai et al. (2008). Additionally, Cai et al. (2010) demonstrated that the difference in feed intake and growth between the low RFI and control lines mostly occurred during the second half of the growth period, past 50 kg body weight.

The main biological factors that contribute to variation in RFI have been partially quantified in mice (McDonald et al., 2009), poultry (Luiting, 1990), and beef cattle (Richardson and Herd, 2004a). As reviewed by Herd and Arthur (2008), in beef cattle, approximately 73% of the variation in RFI is accounted by factors that include activity, feed intake patterns, behavior, stress, digestibility, protein turnover, and tissue metabolism. The importance of these processes for differences in RFI in pigs is unknown. Therefore, the objective of this study was to evaluate the 5th generation of the Iowa State University low RFI and control lines for feed intake, growth performance, body composition, and chemical carcass composition under ad libitum and restricted feed intake. The focuse here was on differences during the early, post wean growth phase. We hypothesized that during the early-mid growth phase 1) carcass composition and 2) predicted maintenance energy will differ between the control and low RFI pigs. It is these differences that appear late in this early growth period that are driving the overall reduced feed intake and improved feed efficiency in our RFI selection lines compared to the control lines.

Materials and Methods

Experimental Design

All animal procedures were approved by the Animal Care and Use Committee of Iowa State University. Using a randomized complete block design, 100 Yorkshire barrows (22.6 ± 3.9 kg) from the 5th generation of the Iowa State University RFI lines, 50 from the line selected for reduced RFI (referred to as the Select line in the remainder) and 50 from the randomly selected Control line, were paired based on age and weight, and each pair was randomly assigned to adjacent individual pens. Within each replicate, littermates were used within each of the two lines. Pigs were allowed to acclimate for three days on ad libitum feeding and had free access to water at all times. Throughout the entire experiment, all pigs received the same diet, which was formulated to meet or exceed nutrient requirements for this size pig (NRC, 1998) over the six-week test period for each treatment (Table 3.1). Following the three day acclimation period, all pigs were fed ad libitum for seven days and average daily feed intake was recorded for each pig (week -1). Thereafter, within each replicate, pairs were randomly allocated to one of four feed intake levels (treatments) with increasing levels of feed restriction to capture differences in growth and maintenance requirements between the lines. The feed intake treatments were: 1) ad libitum (Ad), 2) 75% of feed intake of the Ad Control pigs (Ad75), 3) 55% of feed intake of the Ad Control pigs (Ad55), and 4) a weight stasis (WS) treatment with the goal to maintain static body weight to estimate potential differences in maintenance energy requirements. In the WS treatment, feed intake was individually adjusted to maintain initial body weight. The initial feeding level used for the WS treatment was based on estimated energy requirements for maintenance based on $106BW^{0.75}$, where BW was the pig's body weight on day -1 prior to treatment. The energy required per day to support each pig's maintenance energy requirements was then calculated following National Research Council guidelines for swine (NRC, 1998). Pigs on the WS treatment were weighed twice per week and their feed intake was then immediately adjusted based on weight gain or loss relative to their starting BW.

The experiment was conducted in eleven replicates of 8 or 10 pigs (1 pig per line by treatment combination, plus 1 additional pig per line on the WS treatment for replicates with 10 pigs) and the duration of the test period was six weeks. Pigs on any of the three restricted feed intake treatments were provided two equal portioned meals at 0700 and 1700 hrs each day. Feed allotments for the Ad75 and Ad55 treatments were based on the average daily feed intake (ADFI) in the previous week of the Control line ad libitum fed pigs within each pig's replicate. All pigs were genotyped for the Melanocortin-4 receptor (MC4R) gene following Kim et al. (2000), as it has been shown to be associated with growth, FI and BF.

Performance Traits

All pigs were weighed at the beginning and end of the pre-treatment week (days -7 and -1 of week -1). Week -1 ADFI was calculated as feed offered minus feed refused during week -1 and used to establish feed allotted to pigs on the Ad75 and Ad55 treatments on day 0. Pre-treatment average daily gain (ADG) was based on BW at day -1 and -7. This was the beginning of the six-week test period.

All pigs were weighed individually at the start of the treatment period (day 0), and pigs on the Ad, Ad75, and Ad55 treatments were weighed on day seven of each week until the end of the treatment period (day 42). Pigs on the WS treatment were weighed on days three and seven of each week to adjust feed intake in order to maintain static BW. Weekly ADFI for Ad pigs was calculated as feed offered minus feed refused on day 7 of each week. Average daily gain was calculated for all pigs each week of the treatment period. Ultrasonic measurements of 10th rib backfat (BF) and loin eye area (LEA) were collected on days 0, 14, 28, and 42 of the treatment period. Two 10th rib images were collected by a National Swine Improvement Federation certified technician using an Aloka 500V SSD ultrasound machine fitted with a 3.5 MHz, 12.5 cm, linear-array transducer (Corometrics Medical Systems, Inc., Wallingford, CT).

Upon completion of the performance study, pigs from eight replicates were fasted over night, weighed, anesthetized via an i.v. injection (0.04 mL/kg BW) of a 1:1:1 mixture of Telazol-HCl (Fort Dodge Animal Health, Fort Dodge, IA), Xylazine-HCl (Lloyd Laboratories, Shenandoah, IA USA), and ketamine-HCl (Fort Dodge Animal Health, Fort Dodge, IA). After a surgical plane of anesthesia was reached, pigs were euthanized by exsanguination. Immediately thereafter, weights of the viscera, including stomach and intestinal tract, kidneys, lungs, and heart were obtained, and empty body weight was recorded. Whole carcass weight was recorded after the head was removed. The carcass was then split medially and the right half was frozen at -20 $^{\circ}$C for later chemical analyses. Dressing percentage was calculated as empty BW, divided by live weight.

Carcass Composition

After each frozen half carcass was sectioned, it was twice passed through a mechanical grinder (Buffalo No. 66BX Enterprise) and twice through a Hobart 52 grinder with a 5mm die. The ground carcass was thoroughly mixed and a homogenized sample was collected and stored at -20 $^{\circ}$C for laboratory analysis. Carcass chemical analysis of moisture, protein, lipid, and ash was determined after, samples were thawed and aliquots were freeze dried and re-ground. Briefly, water content was determined in triplicate by drying 8.0 g sub-samples to a constant weight in a Fisher Scientific Isotemp oven. Moisture-free subsamples were placed in a Muffle furnace for determination of ash. Nitrogen was determined in quadruplicate using the Kjeldahl method in a Fisher Scientific digestion and distillation system. Crude protein was calculated by multiplying the nitrogen content by 6.25. Lipid content was determined in duplicate samples of approximately 3.5 g by ether extract using a goldfish Fat Extraction system (AOAC, 1980).

Carcass Energy and Consumed Energy

The gross energy (GE) content of the diet and carcasses was determined in duplicate by adiabatic bomb calorimetry and also calculated based on proximate analysis values for protein and lipid using 5.6 and 9.4 kcal per gram, respectively (Ewan, 2001). To calculate carcass energy using the bomb calorimetry values, carcass dry matter in kg was multiplied by the energy content per kg of carcass. To acquire carcass energy based on protein and lipid, kg of carcass protein and fat were calculated from the carcass composition data and multiplied by their respective energy values (Ewan, 2001).

Statistical Analysis of Performance and Composition Data

All data were analyzed using the MIXED procedure of SAS (SAS, 2007). All models included replicate, line and MC4R genotype as fixed factors. Random effects were included for litter and replicate-by-treatment interaction terms. The litter random effects were included to account for co-variances among litter mates, while the interaction random effects were included to account for pairing of Control and Select line pigs because there was one Control-Select pair for each combination of replicate and treatment. For traits that were analyzed by treatment (see below), the litter and interaction random effects were removed as there were no litter mates within a treatment and replicate accounts for Control-Select pairs when only a single treatment is considered. However, litter was included in the model for the WS treatment because some replicates had two pigs from each line.

Pre-treatment traits of BW at day -7 and day -1, ADFI for week -1, and BF and LEA on day 0 were analyzed as described previously. Starting BW on day -7 was included as an additional covariate for the analyses of week -1 ADFI and average daily gain. Day 0 BW was included as an additional covariate for the analyses of day 0 BF and LEA. Day 0 BW, BF, and LEA were also analyzed across treatments, with additional fixed factors of treatment and the interaction of line-by-treatment and random effects of litter and the interaction of replicate-by-treatment for the starting points in Figures 3.1A, 3.2A, and 3.2B, respectively.

Because of the treatment design, the performance traits of BW, ADFI, BF, and LEA while pigs were on treatment were analyzed as repeated measures separately for each treatment, with day 0 BW as a covariate and additional fixed effects of week and the interaction of line and week. For BF and LEA, in addition to day 0 BW, day 0 BF and day 0 LEA were used as covariates, respectively. For the trait of BW, the repeated measures analysis included time points from day 7 to day 42. Day 0 BW was not included as a time point because it was a covariate. Similarly, the traits of BF and LEA only included time points from day 14 to day 42 because trait observations at day 0 were included as covariates. A first-order autoregressive, AR(1), covariance structure was used to model correlations among pig-specific residuals across time.

The carcass traits of live weight at slaughter, carcass weight, viscera weight, dressing percentage, and chemical carcass composition were analyzed across treatments, with additional fixed effects of treatment and the interaction of line and treatment, day 0 BW as a covariate, and random effects as previously stated. Slaughter BW was included as an additional covariate for carcass and viscera weight. Because of the large differences in slaughter BW between treatments, this covariate was fitted as the pig's BW minus the average slaughter BW for that treatment, such that least square means were computed for the average BW for each treatment.

For carcass energy, day 0 BW, day 0 BF, and day 0 LEA were included as additional covariates to adjust for differences in carcass energy at the start of the test, such that resulting least square means are estimates of differences in retained energy. This analysis assumes that BW, BF and LEA on day 0 are adequate estimates of carcass energy at the start of test. This assumption was validated by analyzing carcass energy by the same model but with ultrasound BW, BF, and LEA at slaughter (day 42) as predictors. This model had an R^2 value of 0.92. Gross energy consumed over the 6-week test period was analyzed separately for each treatment with day 0 BW as a covariate.

Estimation of Line-specific Maintenance Requirements and Efficiency

Maintenance requirements and efficiency of energy retention were estimated by regressing carcass energy on gross energy consumed, following the procedures outlined in Ewan (2001). The carcass energy used in this analysis was adjusted for carcass energy at the start of treatment by adjusting for the effects of day 0 BW, BF, and LEA using regression coefficients obtained from the analysis of carcass energy described previously. To estimate maintenance requirements and efficiency of energy retention, adjusted carcass energy was used as a response variable in a general linear model with fixed effects of line, treatment group, and the interaction of line and treatment group, and covariates of feed energy consumed and its interactions with line and treatment group. Because the linear relationship between energy retained and energy consumed is expected to be consistent for all treatments except for the WS treatment, the Ad, Ad75, and Ad55 treatments were combined into treatment group 1 for this analysis and the WS treatment made up treatment group 2. The interaction of line and treatment group allowed separate estimates of maintenance requirements and efficiency for the two treatment groups. To estimate line specific maintenance requirements and efficiency, the interaction of feed energy consumed with line was included in the model. Finally, to test for separate slopes between the two treatment groups, the interaction of feed energy consumed and treatment group was included in the model. The three-way interaction of feed energy consumed with line and treatment group was included in initial analyses but removed because it was not significant.

Results

Pre-treatment differences

Body weight and feed intake data for week -1, along with day 0 BF and LEA, are in presented in Table 3.2. There was no significant difference in feed consumption between the two lines during this initial data collection period. However, the Select line pigs weighed significantly less than the Control line pigs (23.6 vs. 24.1 kg, respectively, $p < 0.01$, data not shown) and had significantly lower ADG ($p < 0.01$, Table 3.2) after adjusting for day -1 BW. There was no significant pre-treatment difference in BF ($p < 0.34$) and LEA ($p < 0.11$) between the two lines. Day 0 BW was not adjusted for day -7 BW and did not differ between the lines; however, subsequent results were adjusted by including day 0 BW as a covariate in the models. As expected, there were no significant differences ($p < 0.96$) in BW, BF, or LEA between the groups of pigs that were randomly assigned to each treatment (data not shown).

MC4R results

Melanocortin-4 receptor genotyping revealed no significant differences between the two pig lines for the majority of the analyses. This was likely due to the small numbers of animals for the purposes of testing for genotype effects. Genotype for MC4R was, however, left in the model for all analyses. Results for traits for which the effect of MC4R was significant ($p < 0.05$) will be summarized here. Genotype for MC4R tended to be significant for ADFI and ADG in the week pre-treatment. During the week -1 period, ADFI for pigs homozygous for the 2 allele tended to consume the least amount of feed, while heterozygous pigs consumed the most ($p < 0.09$). Over the same treatment period, pigs homozygous for the 1 allele tended to have a higher rate of gain, while pigs homozygous for the 2 allele had the lowest rate of gain ($p < 0.06$). For body weight under the WS treatment, pigs homozygous for the 2 allele had the heaviest BW, while pigs homozygous for the 1 allele had the lightest BW ($p < 0.05$). For LEA under the Ad treatment, heterozygous pigs had the largest LEA, while pigs homozygous for the 1 allele had the smallest LEA ($p < 0.07$). Finally, for carcass fat%, pigs homozygous for the 2 allele had the highest fat%, while heterozygous pigs had the lowest fat% ($p < 0.04$).

Performance and Ultrasound Traits

Least square means for the repeated measures analysis of BW and ADFI over the six week treatment period are in Figure 3.1. These data were analyzed separately for each treatment and adjusted for day 0 BW within treatment. As expected, BW increased as the amount of feed provided increased from treatment WS to Ad. The Ad Select (AdS) pigs tended to consume less feed than the Ad Control (AdC) pigs (1.8 vs. 1.9 kg/d, $p < 0.10$) over the entire 6 week period, with a significant difference in feed intake in weeks 5 ($p < 0.03$) and 6 ($p < 0.04$). Moreover, there was no significant difference in BW between the AdS and AdC pigs for any given week. By study design, the Control and Select line pigs consumed the same amount of feed for the Ad75 and Ad55 treatment. The Ad75 Select line pigs steadily diverged in weight from the Control pigs, with the S75 pigs weighing significantly more than the C75 pigs in weeks 5 ($p < 0.05$) and 6 ($p < 0.02$). Conversely, for the Ad55 treatment, there was no significant difference in body weight between the Select (S55) and Control (C55) pigs. There was no significant difference in body weight between the two lines under the WS treatment during any week. Although the objective of the WS treatment was to keep body weight constant, the main effect of week was highly significant ($p < 0.01$);

although the interaction of line-by-week was not significant, the SWS pigs gained 1.54 ± 0.32 kg from day 7 to day 42 ($p < 0.01$) and the control line only gained 0.67 ± 0.33 kg from day 7 to day 42 ($p < 0.05$). Although not significant ($p < 0.35$), the SWS pigs consumed 4% less feed over the treatment period compared to the CWS pigs.

Least square means from analyses of ultrasonic measurements of BF and LEA over the six week test period are in Figure 3.2. These repeated measures were analyzed separately for each treatment and adjusted for day 0 BW, and for day 0 BF and day 0 LEA, respectively. As expected, both BF and LEA increased with an increase in feed provided by treatment (Figure 3.2A). For the Ad treatment, there was no significant difference in BF ($p < 0.25$) or LEA ($p < 0.34$) between the two lines within any one week. There was no significant difference in BF between lines in the Ad75 treatment, however, the Ad75 Select pigs tended to have a larger LEA at week 6 ($p < 0.10$) compared to the Control pigs. For the Ad55 treatment, there was no significant difference in BF between the two lines except at day 28, when the Select pigs tended to have less BF than the Control pigs ($p < 0.09$). There was no significant difference in LEA between the pig lines when fed at either Ad75 or Ad55.

In the WS treatment, the main effect of week was significant for both BF and LEA ($p < 0.01$), with a significant line-by-week interaction ($p < 0.03$) for BF but not significant for LEA. Due to the severity of feed restriction, both lines lost BF under the WS treatment. Select pigs lost only 0.46 mm in BF from day 14 to day 42 ($p < 0.02$) while the Control pigs lost 1.21 mm from day 14 to day 42 ($p < 0.01$). Surprisingly, Select pigs had an increase of 1.6 cm^2 in LEA from day 14 to day 42 ($p < 0.01$), while Control pigs did not have a significant increase in LEA ($p < 0.13$). However, the interaction of line-by-week was not significant for either BF or LEA. On average, Select pigs on the WS treatment had significantly more BF at day 42 than Control pigs (6.1 vs. 5.4 mm, respectively, $p < 0.04$). Similarly, Select pigs had a 7% larger LEA at day 42 than Control pigs, although this was not significant ($p < 0.17$).

Carcass Traits

The main effect of treatment was highly significant ($p < 0.01$) for all carcass traits, with the exception of dressing percentage, for which there was a tendency for a difference among treatments ($p < 0.08$) (Table 3.3). Note that results for live body weight (Table 3.3) differed slightly from results presented for day 42 BW (Figure 3.1), because only 8 of the 11 replicates were harvested for carcass composition, whereas all 11 replicates were used for performance measures. The main effect of line was significant ($p < 0.01$) only for weight of viscera, with the Select line having 6% less visceral mass compared Control pigs when averaged over treatments. On a within feed treatment basis, differences between lines in viscera mass tended to be lower for the Ad ($p < 0.10$) and Ad55 treatments ($p < 0.08$), with no significant differences for the Ad75 ($p < 0.25$) and WS ($p < 0.15$) treatments. Although other traits did not show significant line effects across treatments, the two lines were significantly different for several specific trait-by-treatment combinations. Select pigs had significantly lower live weights compared to the Control pigs under the Ad treatment ($p < 0.01$). Furthermore, under the WS treatment, Select pigs had significantly higher dressing percentage than Control pigs ($p < 0.01$). Low RFI pigs had significantly lower visceral mass than Control pigs for each treatment, with a tenancy for a difference for the Ad55 treatment.

Chemical Carcass Composition

Percentages of the main chemical components of carcass protein, lipid, ash, and water summed to 100.6±0.21% of the subsample weight, which confirms the accuracy of the procedures used (Table 3.3). The main effect of treatment was significant for all components ($p < 0.01$). With an increase in feed restriction, protein% and water% increased, while fat% decreased. The treatment effect of ash% was driven by the WS treatment, which had the greatest ash%. For all traits, the main effect of line across treatments was not significant ($p < 0.21$); however, the two lines were significantly different for some specific trait-by-treatment combinations. For protein%, the line-by-treatment interaction was significant ($p < 0.02$). The Select line had greater protein% than the Control within the Ad ($p < 0.34$), Ad75 ($p < 0.11$), and WS ($p < 0.04$) treatments, and the Select line had less protein% than the control within the Ad55 treatment ($p < 0.07$). For fat%, the Select line had significantly less ($p < 0.03$) than the Control for Ad, with no significant line difference for the other treatments. There were no significant differences between the two lines in ash% within any treatment, except for Ad55, for which the Select line tended to have less ash% than the Control line ($p < 0.08$). AdS had significantly more water% compared to the Control ($p < 0.03$), with no significant difference between lines for the other treatments.

Analysis Energy Consumed versus Retained

The effects of treatment and line on carcass energy when using results from calorimetry (BCE) are in reported Table 3.3. The main effect of treatment was highly significant, with an increase in feed restriction resulting in a decrease in carcass energy ($p < 0.01$). The line effect revealed that the Select line pigs had 3 Mcal less carcass energy than the Control pigs but this was not significant ($p < 0.27$). However, a line effect on carcass energy was observed for the Ad treatment ($p < 0.02$), with Select line pigs having lower carcass energy.

Similar to ADFI, gross energy consumed (GEC) was analyzed separately for each treatment because of the nature of the treatments imposed and, thus, the main effects of treatment and the interaction of line and treatment were not estimates. Again, in contrast to ADFI (Figure 3.1B), only 8 pigs per treatment and line were evaluated for GEC (Table 3.3). No significant differences were found in GEC between the Select and Control lines for the Ad and WS treatments, although the Select line tended to have lower GEC for both treatments (Table 3.3). By study design, pigs within the Ad75 and Ad55 treatments consumed the same amount of energy, respective to treatment.

Line-specific Predicted Maintenance Requirements and Efficiency

Figure 3 shows a scatter plot of carcass energy adjusted for Day 0 BW, BF, and LEA vs. energy consumed and fitted regression lines of adjusted carcass energy on energy consumed by line and treatment group (WS versus all other treatments). The fitted regression lines had an R^2 of 0.95, indicating an excellent fit. However, one Ad Control pig appeared to be an outlier and this pig affected results. Thus, data were analyzed both with and without this pig. In general, carcass energy increased as energy intake increased, as expected. However, this increase, which is quantified by the slopes of the regression lines, tended ($p < 0.08$) to be different for the WS treatment than the other three treatments, which is why separate lines were fitted by treatment group. When the outlier Ad Control pig was removed, this difference in slopes between treatment groups became significant ($p < 0.05$). The difference between the intercepts for the Select WS and Control WS lines, i.e. the difference in retained energy extrapolated to zero feed intake, is an estimate of the difference in maintenance requirements between the two lines. There was no significant difference between the intercepts for the two lines ($p < 0.96$), indicating no significant difference in maintenance requirements. However, when the outlier AdC pig was removed, the p-value dropped from 0.96 to 0.64; although not significant, the difference in intercepts was 1.8 ± 3.8 Mcal, with the Select line having a higher intercept, indicating potentially lower maintenance requirements. The slopes of the regression lines are estimates of the efficiency with which feed energy consumed above maintenance is retained (i.e. a steeper slope corresponds to greater energy retention). Although not significant ($p < 0.16$), the slope for the Select line was 0.043 greater, suggesting it to have greater efficiency than the Control line. However, this was primarily driven by the outlier Ad Control pig. When this pig was excluded, the difference of the slopes between the two lines dropped to 0.007 and was not significant ($p < 0.81$). For these analyses, the 3-way interaction of feed energy consumed by line and treatment group was dropped from the model due to its large p-value (0.73), thus the differences in the slopes between the two lines applied to both treatment groups

Discussion

The current study aimed to evaluate a low residual feed intake line against a Control line at a young age for differences in carcass composition and predicted maintenance requirements. Pigs in the current study were from the fifth generation of two selection lines of Yorkshire pigs, where pigs selected for low residual feed intake and a randomly bred control line were evaluated for differences in residual feed intake under group feeding from

~45 to 110 kg (Cai et al., 2008). As expected based on results from Cai et al. (2008), under ad libitum feeding, the Select line pigs consumed less feed than the Control line. However, in contrast to Cai et al. (2008), who reported slightly lower growth for the Select line, rate of gain was not different from the Control line. This difference in results for growth can be attributed to the different environments, as pigs in the current study were individually penned leading to a faster rate of gain (de Haer and de Vries, 1993). When feed was restricted to 75 and 55% of ad libitum, pigs from the Select line had a slightly greater weight gain on the same amount of feed, which suggests that the Select line has reduced maintenance requirements or is more efficient at tissue deposition. The trait RFI, as defined by Koch et al. (1963), is the observed feed intake minus expected feed intake based on average requirements for maintenance and growth. Therefore, by feeding the two lines identically restricted amounts of feed, pigs with reduced maintenance requirements or increased efficiency of tissue deposition are expected to have greater growth. The WS treatment was designed to assess the difference in maintenance requirements of the two lines, although this is just a crude indicator of maintenance requirement, because of changes in body composition. Although the aim of the WS treatment was to keep body weight constant body weight slightly increased for both lines from day 0 to day 42. However, Select line pigs had significantly greater increases in body weight than Control line pigs, with no significant difference in feed intake. Collectively, these results indicate that selection for reduced residual feed intake results in greater feed efficiency.

Estimates of genetic correlations between RFI and backfat thickness are generally positive in pigs, ranging from 0.07 to 0.77 (Gilbert et al., 2007; Hoque et al., 2009; Johnson et al., 1999). In market weight pigs of the Iowa State University RFI selection lines, Bunter et al. (2010) found a positive genetic correlation between RFI and BF (0.20). Furthermore, a study that looked at BF accretion rates using real-time ultrasound found that the variation in BF depth increased with body weight (Moeller and Christian, 1998), indicating that BF does not differ significantly in young pigs. In the current study, BF results were unclear. There was no significant difference in BF between the two lines within treatments, when analyzed using repeated measures, which may be explained by the young age. However, contradictory to results from the repeated analysis of BF (Figure 2A), likely due to the different models and assumptions behind the covariate of day 0 backfat, under *ad libitum* feeding, the Select line had significantly less BF at day 42 (Table 3). Furthermore, there was a significant difference in BF between the two lines under the weight stasis treatment, under which the Select line pigs lost less BF (Figure 3.2A) and tended to have more BF at day 42 than the Control pigs (Table 3.3). This indicates that the Select line prioritizes energy differently to maintain energy stores under severe feed restriction.

Genetic correlations between RFI and LEA in pigs have generally been found to be negative, ranging from -0.18 to -0.60 (Cai et al., 2008; Hoque et al., 2009; Johnson et al., 1999). Cai et al. (2008) found that the select line had greater LEA than the control. In the current study, the select line had larger LEA than the control, although not always significant. From these results, the Select line appears to be leaner than the Control line, as there was no significant difference in BF and increased LEA. Interestingly, for the WS treatment, the Select line pigs had more BF, a slightly larger LEA, and consumed slightly less feed, indicating that the Select line is partitioning less of the consumed energy for maintenance requirements than the control and more towards growth.

Live weight was not significantly different between the two lines within any of the treatments except under ad libitum feeding, where Select pigs weighed significantly less than Control pigs. This difference may largely be explained by two factors. First, in Figure 3.1A, the Control line had a slightly heavier BW, although it was not significant. A second explanation is that only 8 of the 11 replicates were slaughtered, whereas, weekly BW was measured for all 11 replicates. Furthermore, there were no significant differences in carcass weight after adjusting for live weight. Given the previous results of no significant differences in slaughter and carcass weights, there were no significant differences in dressing percentage between lines within any treatment, except for the WS treatment, for which Select line pigs had a 4% greater dressing percentage. This difference can be attributed to the tendency for a difference in carcass weight and slightly lower visceral mass. Selection for low RFI resulted in lighter visceral weights which, in the latter part of the growing phase, may ultimately increase dressing percentage and profit for the producer. Viscera, compared to muscle, is energetically expensive to maintain (Noblet et al., 1999). Therefore, lower visceral mass in the Select line appears to contribute to the difference in feed intake and increased feed efficiency compared to the Control.

A study that divergently selected Yorkshire pigs for low and high-fat, along with a Duroc line divergently selected for low and high-fat, found that pigs selected for low-fat had reduced ether extract percentage (fat%) compared to the pigs of the high-fat line at 19.0 kg of body weight (Brooks et al., 1964). In the current study, under ad libitum feeding, the Select line had 2.2% less fat than the control but 2% more water, which supports our hypothesis that carcass composition between the two lines is different at a young age. Therefore, the Select line makes up in water what it is lacking in fat compared to the control. However, our hypothesis is not supported in the treatments where feed was restricted, as chemical carcass composition did not differ between the lines.

In beef cattle, steer progeny form low RFI parents had less BF and more protein than progeny from high RFI parents (Richardson et al., 2001). These differences in steer progeny chemical carcass composition, however, accounted for only 5% of the difference in RFI (Richardson et al., 2001). To evaluate the extent to which differences in feed intake could be explained by differences in carcass composition in our study, net energy consumed was estimated to be 56% of gross energy consumed (Oresanya et al., 2008), using the LSM of Table 3.3. Then, line differences in net energy consumed were compared to estimated line differences in carcass energy retained, using SLM (Table 3.3). In the ad libitum treatment, the line difference in net energy consumed was (318.4 – 292.8)*0.56 = 14.3 Mcal, whereas the line difference in retained energy was 122.1-109.6 = 12.5. To estimate the extent to which the difference in carcass composition explains the difference in consumed energy, retained energy is divided by net energy consumed. Here, the difference in carcass composition may explain 87% of the difference in consumed energy, given our assumption that net energy intake is 56% of gross energy consumed is correct. For the other treatments, the line difference for retained energy was larger than the difference in consumed energy. Overall, it appears that carcass composition does indeed explain a substantial portion of the difference in feed intake. Furthermore, this difference in carcass composition can be attributed largely to the difference in fat content.

Maintenance energy requirements are believed to be associated with RFI. Selection for lower RFI resulted in lower maintenance requirements in beef cattle (Herd and Bishop, 2000). Based on the intercepts from the regression analysis (Figure 3.3), there was no significant difference in maintenance requirements between the two lines; only a trend for the low RFI pigs under weight stasis feeding to have lower maintenance requirements. As discussed previously, this trend for the select line to have reduced maintenance requirements is supported by the fact that, under restricted feeding, the Select line had slightly heavier body weights, and slightly less feed to maintain static body weight. However, this lack of significant difference can be attributed to the tight pattern and little variation between the two lines on the weight stasis treatment regarding growth and feed intake. The slopes presented in Figure 3.3A indicate that the Select line is more efficient in retaining energy consumed, as quantified by the steeper slope for the Select line than the Control line. After removing the ad libitum Control pig that appeared to be an outlier, the Select line had a slightly steeper slope than the Control. Interestingly, the Select line was more efficient in retaining energy consumed yet the Control line contained more fat. This indicates a difference in the partitioning of the energy consumed, as the Control line appears to be partitioning energy towards fat deposition, while the Select line may be portioning energy more towards protein deposition, ultimately leading to a leaner carcass. Because the maintenance results are strictly estimates, further work is needed to investigate the true differences in maintenance requirements and energy partitioning. Nonetheless, selection for low RFI in Yorkshire pigs had reduced feed intake under ad libitum feeding, with limited effects on growth rates and carcass yield. Under restricted feeding, the select line had heavier carcass weights than the control, indicating that the low RFI line is more efficient at converting the energy consumed into tissue. However, carcass composition appears to be one of the main biological factors that contributed to the difference in RFI between the two lines.

Implications

Results of this study show that selection for low RFI improved feed efficiency during the early post-weaning growth phase, with limited differences in growth. Reductions in feed consumption in the early part of the growth phase is promising to the producer, as reduction in feed cost will last through the life of the pig. The increased feed efficiency observed in the Select line may largely be due to differences in carcass composition and maintenance energy requirements.

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Table 3.1. Diet Composition

Ingredient	%
Corn, Grain	59.69
Soybean Meal-48	22.98
Soybean Hulls	7.72
Menhaden Meal	3.50
Meat & Bone Meal	3.00
Soybean Oil	1.50
Vitamin Mix[1]	0.50
Dicalcium Phosphate	0.37
Salt	0.35
L-Lysine HCl	0.12
Limestone	0.11
Mineral Mix[2]	0.10
Selenium	0.05
Calculated analysis, %	
Crude Protein	21.25
Lysine	1.20
Calcium	0.70
Available Phosphorus	0.35
Metabolizable energy, Kcal/g	3265.00

[1] Vitamin mix donated by DSM Nutritional Products, Inc., Ames IA 50010 and provided the following per kilogram of diet: vitamin A, 4,409 IU; vitamin E, 22 IU; vitamin D3, 1,102; niacin, 33mg, D-pantothenic acid, 18 mg; riboflavin, 6.6 mg.

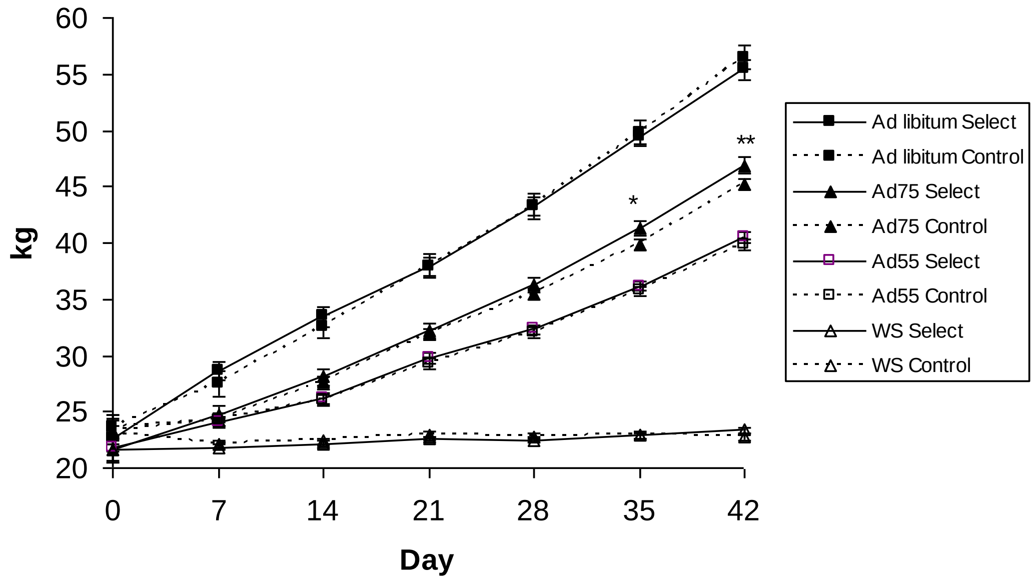
[2] Mineral mix provided the following per kilogram of diet: Zn, 90 mg as ZnO; Fe_2SO_4; Cu, 10.5 mg as CuO; Mn, 36 mg as MnO_2; I, 1.2 mg as CaI.

Table 3.2. Least square means ± SEM for body weight and feed intake of pigs from the low residual feed intake (RFI) and control lines at the start and end of the week prior to dietary treatment, and for ultrasonic backfat and loin eye area at the start of treatment. n = 50 pigs per line.

Item	Low RFI line	Control line	p-value
Pre-treatment week (Day -7 to -1)			
Start weight, kg	19.2 ± 0.75	20.3 ± 0.74	0.3
Feed intake, kg/d	1.08 ± 0.03	1.13 ± 0.03	0.19
Daily gain, g/d[1]	596.0 ± 15.0	659.0 ± 16	< 0.01
On-test (Day 0)			
Body weight, kg	21.9 ± 0.81	23.5 ± 0.80	0.17
Backfat, mm	8.03 ± 0.21	8.30 ± 20	0.34
Loin eye area, cm^2	9.63±0.37	10.4±0.36	0.11

[1] Adjusted for Start weight (day -7)

A) Body Weight



B) Average Daily Feed Intake

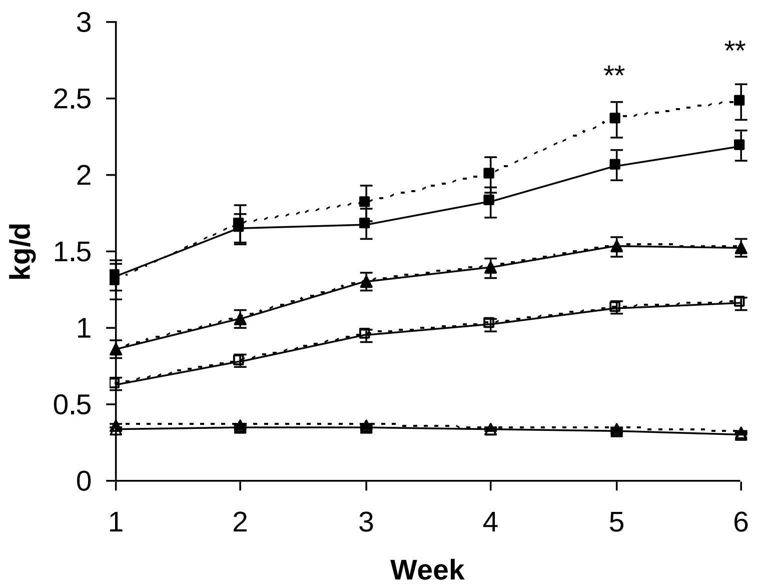
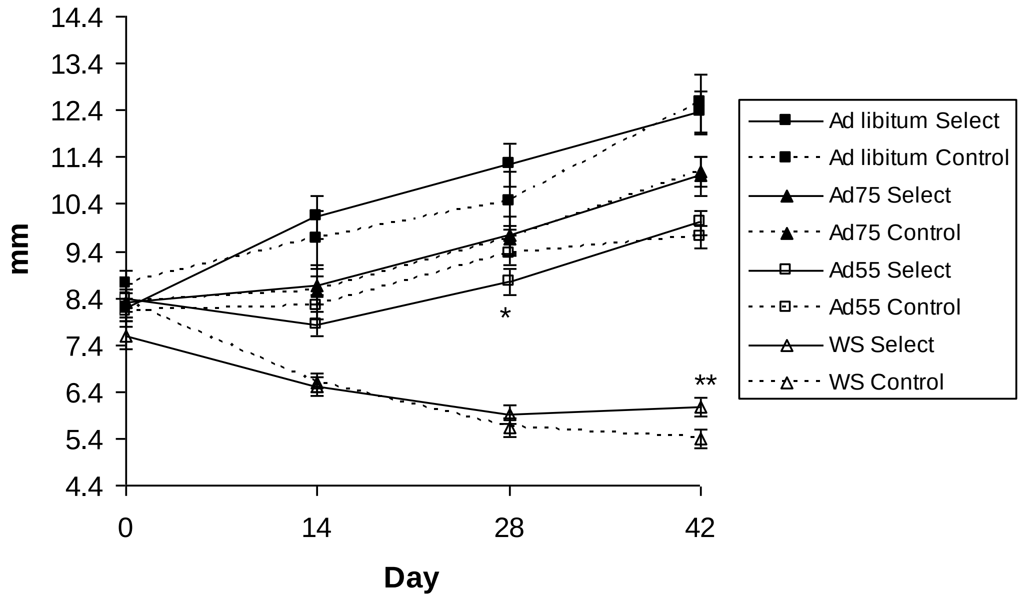


Figure 3.1. Effects of diet restriction on body weight (A) and average daily feed intake (B) of low residual feed intake and control finisher barrows. Panel A represents least square means ± SEM for body weight every 7 days starting with day 7 (Day 0 was used as a covariate). Panel B represents least square means ± SEM for weekly average daily feed intake. n = 10 per line for the ad libitum, 75% of ad libitum (Ad75), and 55% of ad libitum (Ad55) treatments, and n = 20 per line for the weight stasis (WS) treatment.

A) Backfat



B) Loin Eye Area

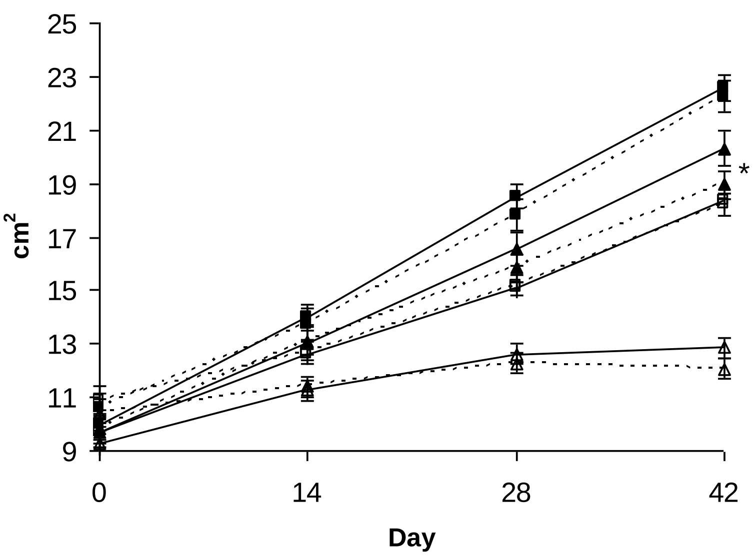


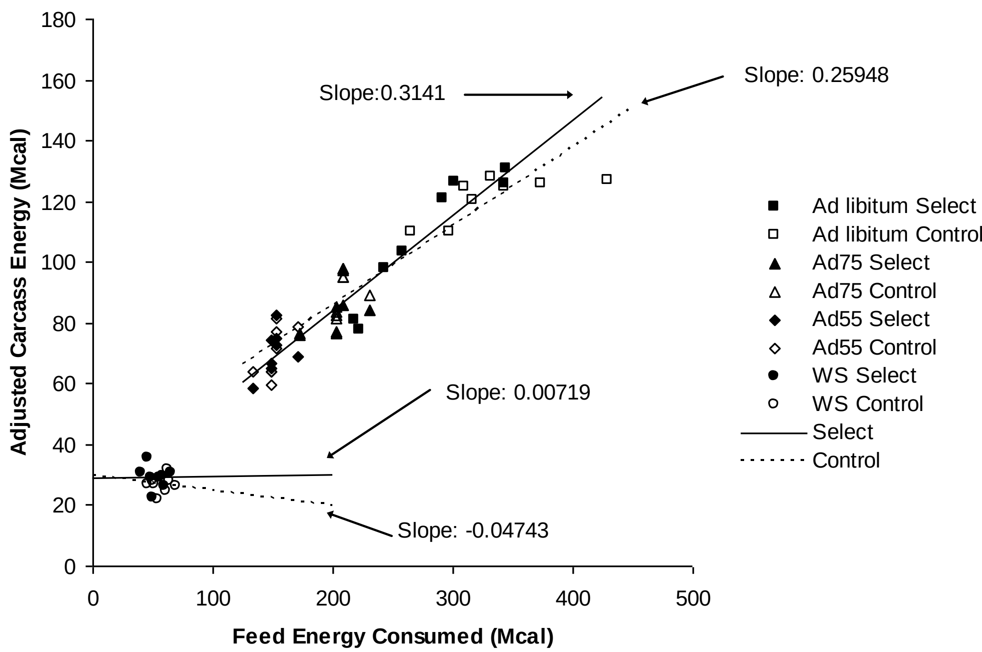
Figure 3.2. Effects of diet restriction on backfat (A) and loin eye area (B) of low residual feed intake and control finisher barrows. Panel A represents backfat every 2 weeks (least square means ± SEM). Panel B represents loin eye area every 2 weeks (least square means ± SEM). n = 10 per line per treatment for the treatments of ad libitum, 75% of ad libitum (Ad75), and 55% of ad libitum (Ad55), and n = 20 per line for the weight stasis (WS) treatment for both analyses. Repeated measures analysis begins with day 14 for both panels, as day 0 was used as a covariate for the respective traits along with day 0 body weight.

Table 3.3. Least square means for treatment (T) and line (L) on body and carcass composition for the eight pigs per line and treatment that were harvested[1]

Carcass Item	Ad libitum Select	Ad libitum Control	75% of Ad libitum Select	75% of Ad libitum Control	55% of Ad libitum Select	55% of Ad libitum Control	Weight Stasis[13] Select	Weight Stasis[13] Control	Line difference[2]	p –value L	p –value T	p –value L*T[3]
Live weight, kg[7]	55.0±1.0[d]	59.1±1.1[e]	49.3±1.1[c]	48.1±1.0[c]	42.7±1.0[b]	41.3±1.1[b]	24.4±1.1[a]	24.1±1.0[a]	0.33±0.72	0.65	0.01	0.02
Day 42 BF, mm[9]	12.4±0.33[d]	13.7±0.34[e]	11.2±0.36[c]	11.0±0.33[c]	10.0±0.34[b]	9.5±0.34[b]	6.3±0.29[a]	5.5±0.28[a]	0.0±0.23	0.90	0.01	0.01
Day 42 LEA, sq. cm[10]	22.7±0.54[d]	23.0±0.56[d]	20.0±0.58[c]	19.3±0.56[bc]	18.3±0.55[b]	17.8±0.56[b]	12.8±0.48[a]	12.2±0.48[a]	-0.40±0.36	0.27	0.01	0.78
Carcass Weight, kg[4, 8]	46.3±0.39[d]	45.5±0.38[d]	37.8±0.40[c]	37.6±0.36[c]	32.9±0.36[b]	33.3±0.39[b]	19.8±0.37[a]	18.8±0.36[a]	-0.40±0.29	0.19	0 .01	0.20
Viscera, kg[5, 8]	9.7±0.26[cd]	10.3±0.26[c]	9.6±0.27[cd]	10.0±0.24[c]	8.4±0.24[b]	9.0±0.26[bd]	5.2±0.25[a]	5.7±0.24[a]	0.55±0.19	0.01	0.01	0.95
Dressing %[6, 7]	0.80±0.01[a]	0.79±0.01[a]	0.78±0.01[a]	0.78±0.01[a]	0.78±0.01[a]	0.80±0.01[a]	0.83±0.01[b]	0.79±0.01[a]	-0.01±0.01	0.40	0.08	0.01
Chemical Composition, % of Carcass												
Water, %[7]	60.8±0.66[e]	58.8±0.67[f]	62.6±0.69[cd]	62.1±0.65[de]	64.1±0.65[bc]	64.1±0.69[b]	72.4±0.66[a]	72.6±0.64[a]	-0.57±0.64	0.39	0.01	0.13
Protein, %[7]	18.2±0.23[bc]	17.8±0.24[c]	18.5±0.25[bc]	17.9±0.23[c]	18.0±0.23[bc]	18.7±0.25[b]	20.4±0.24[a]	19.7±0.23[a]	-0.24±0.22	0.29	0.01	0.01
Fat, %[7]	18.8±0.70[d]	21.0±0.71[e]	16.4±0.74[bc]	17.6±0.68[cd]	15.4±0.68[b]	14.9±0.74[b]	4.2±0.70[a]	4.7±0.68[a]	0.83±0.65	0.21	0.01	0.16
Ash, %[7]	3.1±0.11[ab]	3.0±0.11[b]	3.1±0.11[ab]	2.9±0.11[b]	2.9±0.11[b]	3.2±0.11[ab]	3.4±0.11[a]	3.4±0.10[a]	0.00±0.08	0.96	0.01	0.19
Carcass Energy, Mcal/pig												
CE[11]	109.6±3.5[d]	122.1±3.7[e]	87.5±3.7[c]	88.0±3.5[c]	71.1±3.5[b]	72.5±3.9[b]	29.6±3.6[a]	27.2±3.5[a]	-3.0±2.7	0.27	0.01	0.18
GEC[12]	292.8±13.8	318.4±13.8	204.7±0.0	204.7±0.0	150.8±0.0	150.8±0.0	54.0±1.0	56.4±1.0	--	--	--	--

[a,b,c,d,e,f] different letters in a row represent significant differences at $p < 0.05$
[1] values are least square means based on 8 pigs per line per treatment
[2] difference of control minus select
[3] interaction of line by treatment
[4] carcass equals empty body weight, including head and hair
[5] viscera includes entire intestinal tract with contents, kidney, heart, and lungs
[6] dressing percentage is carcass weight as a percent of slaughter weight
[7] analysis included week 0 body weight as a covariate
[8] analysis included week 0 body weight and adjusted slaughter weight (average slaughter body weight within each treatment minus individual pig's slaughter body weight) as covariates
[9] analysis included day 0 body weight and day 0 backfat
[10] analysis included day 0 body weight and day 0 loin eye area
[11] carcass energy determined from protein and lipid values of 5.6 and 9.4 kcal/g, respectively
[12] gross energy consumed over the 6 week test period (analyzed per treatment)
[13] tendency for a difference at $p < 0.10$ for the traits of day 42 BF and carcass weight

A.



B.

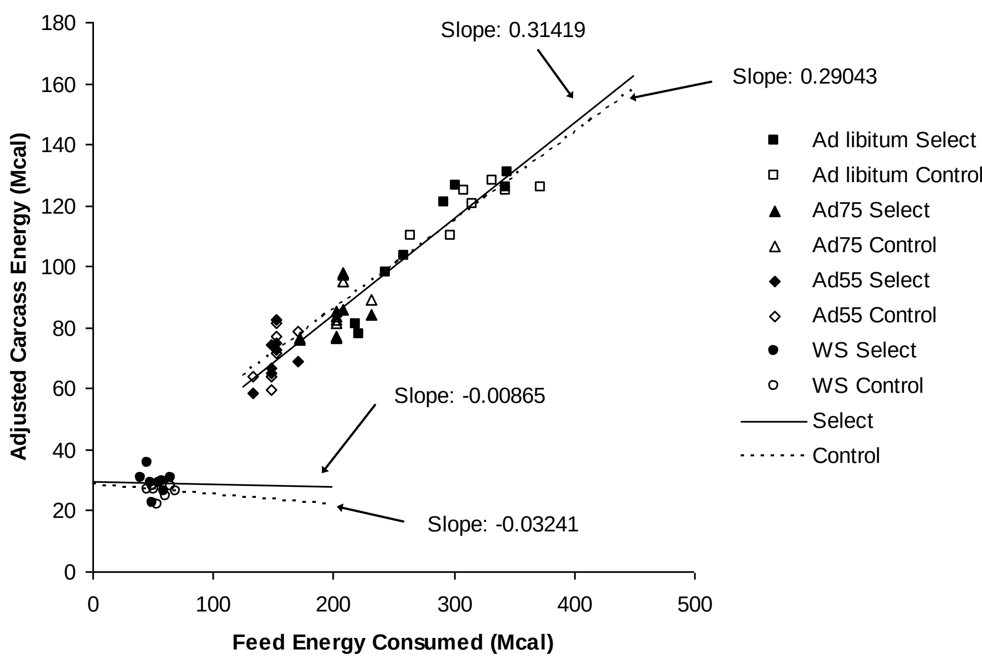


Figure 3.3. Carcass energy, adjusted for initial carcass energy, against total feed energy consumed over the six week test period. Panel A represents results with all pigs included (n = 8 per line per treatment). Panel B represents results after excluding one ad libitum control pig, which appeared to be an outlier.

CHAPTER 4. EFFECTS OF AD LIBITUM AND RESTRICTED FEED INTAKE ON GROWTH PERFORMANCE AND BODY COMPOSITION OF YORKSHIRE PIGS SELECTED FOR REDUCED RESIDUAL FEED INTAKE[1]

A paper to be submitted to the Journal of Animal Science

N. Boddicker[2], N. K. Gabler[3], M. E. Spurlock[4], D. Nettleton[5] and J. C. M. Dekkers[6]

Abstract

Residual feed intake (RFI), defined as the difference in the observed and expected feed intake while accounting for growth and backfat, has gained much attention but little is known about why pigs selected for reduced RFI are more efficient. To this end, a line of Yorkshire pigs selected for reduced RFI was developed. The objective of this study was to evaluate the 5th generation of this 'select' line against a randomly selected control line for performance, carcass and chemical carcass composition, and overall efficiency towards the latter part of the growth phase. Eighty barrows, 40 from each line, were paired by age (~132 d) and weight (74.8±9.9kg), and randomly assigned to 1 of 4 feeding treatments in 10 replicates: 1) ad libitum (Ad), 2) 75% of Ad (Ad75), 55% of Ad (Ad55) and weight stasis

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[1] This project was funded by the National Pork Checkoff and the Iowa Pork Producers Association. Funds for development and maintenance of the selection lines were from the Iowa Agriculture and Home Economics Experiment Station through the Center for Integrated Animal Genomics, Iowa State University, (Project No. 3600) and supported by Hatch Act and State of Iowa Funds.
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(WS), with weekly adjustments in intake to keep body weight (BW) constant for each pig. Pigs were individually penned (group housing was used for selection) and on treatment for 6 weeks. Initial BW did not differ between the lines ($p < 0.49$). The Ad low RFI pigs consumed 10% less feed ($p < 0.09$) than the Ad Control with no significant difference in BW ($p < 0.80$) and slight differences in carcass fat composition ($p < 0.20$) and backfat ($p < 0.11$), which resulted in significantly lower carcass energy ($p < 0.03$). Under restricted feeding, the low RFI line had an increase in BW ($p = 0.10$) while consuming the same ration of feed as the control line with no significant difference in chemical carcass composition and lower visceral weights, which was significant for the Ad75 treatment ($p < 0.01$). Under WS feeding the low RFI pigs consumed 7.6% less feed overall ($p = 0.21$) and 18% less feed at the end of the 6 weeks ($p < 0.08$), to maintain static BW with no significant difference in chemical carcass composition compared to the control. Overall, the low RFI pigs had lower visceral weight ($p < 0.02$) and a higher dressing percentage ($p < 0.03$) compared to the control. Using regression, the reduced RFI pigs had reduced energy retention ($p < 0.04$) and feed energy utilization ($p < 0.34$); however, appeared to have reduced maintenance requirements ($p < 0.13$). In conclusion, selection for reduced RFI decreases feed intake with no significant difference in growth performance, reduced backfat, increased dressing percentage, and lower maintenance requirements. All of these traits are appealing to the producer which results in increased profits in the production setting.

Introduction

Profitability of pork production heavily depends upon the cost of feed and the efficiency with which pigs utilize feed energy for maintenance and growth. Residual feed intake (RFI) is a unique measure of feed efficiency which accounts for growth and backfat, and is calculated as observed minus expected feed intake (Kennedy et al., 1993; Koch et al., 1963; Luiting, 1990). In swine, RFI has been shown to be moderately heritable, with estimates ranging from 0.15 to 0.38 (Cai et al., 2008; Gilbert et al., 2007; Hoque et al., 2009; Nguyen et al., 2005). To investigate the genetic and biological basis of RFI, a selection experiment for reduced RFI (i.e., improved feed efficiency) in purebred Yorkshire pigs was undertaken at Iowa State University. After four generations, selection responses were evaluated by Cai et al. (2008) under group pen and ad libitum feeding conditions; gilts from the low RFI line consumed substantially less feed (165 g/d) but also had a slightly lower growth rate (33 g/d) and backfat (1.99 mm) relative to gilts from the randomly selected control. The difference in RFI was 96 g/d. The main biological factors that contribute to RFI have been partially quantified in mice (McDonald et al., 2009), poultry (Luiting, 1990), pigs (Boddicker et al., 2010), and beef cattle (Richardson and Herd, 2004b) and more recently reviewed by Herd and Athur (2008). In beef cattle, approximately 73% of the variation in RFI is accounted by factors which may include activity, feed intake patterns, behavior, stress, digestibility, protein turnover, and tissue metabolism (Herd and Arthur, 2008). In pigs, the difference in feed intake between low RFI and control pigs at a young age can partially be contributed to carcass composition. Aside from these findings from Boddicker et al. (2010), the importance of these processes for RFI in pigs is relatively unknown. Furthermore, Cai et al. (2010) reported divergence in FI and BW at 110 d and 70 kg, respectively, between a low RFI line and randomly selected control line. Therefore, the objective of this study was to evaluate the 5th generation of the Iowa State University low RFI and control lines for feed intake, growth performance, body composition, and chemical carcass composition under ad libitum and restricted feed intake towards the end of the growth curve. The latter included feeding at a level required to maintain a constant body weight. We hypothesized that, compared to the control line, pigs from the low RFI line would have 1) lower feed intake under ad libitum feeding but a similar rate of gain and carcass composition, 2) a greater rate of gain under restricted feeding, with similar carcass composition, and 3) require less feed to maintain constant body weight.

Materials and Methods

Study Design

All animal procedures were approved by the Animal Care and Use Committee of Iowa State University. Using a randomized complete block design, 80 Yorkshire barrows (74.8 ± 9.9 kg) from the 5th generation of the Iowa State University RFI lines, 40 from the low RFI line and 40 from the randomly selected control line, were paired based on age and weight, and each pair was randomly assigned to contiguous individual pens. Pigs were allowed to acclimate for three days on ad libitum feeding and had free access to water at all times. Following the acclimation period, all pigs were fed ad libitum for seven days and ad libitum feed intake was established (week -1). Pairs were then randomly allocated to one of four feed intake treatments: 1) ad libitum (Ad), 2) 75% of feed intake of the Ad Control pigs (Ad75), 3) 55% of feed intake of the Ad Control pigs (Ad55), and 4) a weight stasis (WS) treatment. In the WS treatment, feed intake was individually adjusted to maintain initial body weight. The experiment was conducted in ten replicates of 8 pigs (1 pig per line by treatment combination) and the duration of the test period was six weeks. All pigs received the same diet, which was formulated to meet or exceed nutrient requirements for this size pig (NRC,

1998) over the six-week test period (Table 4.1). Pigs on restricted feed intake treatments were provided two equal portioned meals at 0700 and 1700 hrs each day. Feed allotments for the Ad75 and Ad55 treatments were based upon the average daily feed intake (ADFI) of the control line Ad fed pigs in the previous week within each pig's replicate. The initial feeding level used for the WS treatment was based on estimated energy requirements for maintenance based on $106BW^{0.75}$, where BW was the pig's body weight on day -1 prior to treatment. The energy required per day to support each pig's maintenance energy requirements was then calculated following National Research Council guidelines for swine (NRC, 1998). Pigs on the WS treatment were weighed twice per week and their feed intake was adjusted based on weight gain or loss relative to their starting BW. All pigs were genotyped for the Melanocortin-4 receptor (MC4R) gene following Kim et al. (2000), as it is associated with growth, FI, and BF.

Performance Traits

All pigs were weighed at the beginning and end of the pre-treatment week (days -7 and -1, of week -1). Week -1 ADFI was based on feed offered minus feed refused for each pig during week -1 and used to determine day 0 feed allotted for the pigs on the Ad75 and Ad55 treatments. Pre-treatment average daily gain (ADG) was based on BW at day -7 and day -1. On day -1, pigs were fasted overnight and a fasting blood sample was collected, representing the beginning of the six-week test period.

All pigs were weighed individually at the start of the treatment period (day 0), and pigs on the Ad, Ad75, and Ad55 treatments were weighed weekly thereafter until the conclusion of the treatment period (day 42). Pigs on the WS treatment were weighed on day three and seven of each week to adjust feed intake to maintain static BW. ADFI for the Ad pigs was calculated as feed offered minus feed refused every seven days. Average daily gain was calculated for each week of the treatment period. Ultrasonic measurements of 10^{th} rib backfat (BF) and loin eye area (LEA) were collected on days 0, 14, 28, and 42 of the test period. Two 10^{th} rib images were collected by a National Swine Improvement Federation certified technician using an Aloka 500V SSD ultrasound machine fitted with a 3.5 MHz, 12.5 cm, linear-array transducer (Corometrics Medical Systems, Inc., Wallingford, CT).

Upon completion of the performance study, pigs from eight replicates were fasted over night, weighed, anesthetized via an i.v. injection (0.04 mL/kg BW) of a 1:1:1 mixture of Telazol-HCl (Fort Dodge Animal Health, Fort Dodge, IA) Xylazine-HCl (Lloyd Laboratories, Shenandoah, IA USA), and ketamine-HCl (Fort Dodge Animal Health, Fort Dodge, IA). After a surgical plane of anesthesia was reached, pigs were euthanized by exsanguination. Immediately thereafter, visceral weights, including stomach and intestinal tract (both with digesta), kidneys, lungs and, heart were obtained, and empty body weights recorded. The head was removed and the carcass weight was recorded. The carcass was then split medially and the right half was frozen at -20 ºC for later chemical analyses. Dressing percentage was calculated as the empty BW, including the head, divided by live weight at harvest.

Carcass Composition

For chemical analysis, each frozen half carcass was sectioned, twice passed through a mechanical grinder (Buffalo No. 66BX Enterprise) and twice through a Hobart 52 grinder with a 5mm die. The ground carcass was thoroughly mixed and a homogenized sample was collected and stored at -20 ºC for laboratory analysis. For analyses, samples were thawed and aliquots were freeze dried and re-ground for determination of moisture, protein, lipid, and ash. Briefly, water content was determined in triplicate by drying 7.5 g sub-samples to a constant weight in a Fisher Scientific Isotemp oven. Moisture-free subsamples were placed in a Muffle furnace for determination of ash. Nitrogen was determined in quadruplicate using the Kjeldahl method in a Fisher Scientific digestion and distillation system. Crude protein was calculated by multiplying the nitrogen content by 6.25. Lipid content was determined in duplicate samples of approximately 3.5g by ether extract using a goldfish Fat Extraction system (AOAC, 1980).

Carcass Energy and Consumed Energy

The gross energy (GE) content of the diet and carcasses was determined in triplicate by adiabatic bomb calorimetry and also calculated based on proximate analysis values for protein and lipid using 5.6 and 9.4 kcal per gram, respectively (Ewan, 2001). To calculate carcass energy using the bomb calorimetry values, carcass dry matter was calculated in kg and multiplied by the energy content per kg of carcass. To acquire carcass energy based on protein and lipid (Ewan, 2001), kg of protein and fat were calculated from the carcass composition data and multiplied by their respective energy values.

Statistical Analysis

All data were analyzed using the MIXED procedure of SAS (SAS, 2007). All models included replicate, line, and MC4R genotype as fixed factors. Random effects were included for litters and replicate-by-treatment interaction terms. The litter random effects were included to account for co-variances among litter mates while the interaction random effects account for pairing of Control and Select animals because there was one control-select pair for each combination of replicate and treatment. However, when traits were analyzed within each treatment, the litter and interaction random effects were removed as there were no litter mates within a treatment and the replicate effects alone already account for control-select pairs when only a single treatment is considered.

Pre-treatment traits of BW at day -7 and day -1, ADFI for week -1, and BF and LEA on day 0 were analyzed as discussed previously; however, the replicate-by-treatment interaction terms were not included as random effects because of the absence of treatment in the pre-treatment trait model. Starting BW on day -7 was included as an additional covariate for day -1 BW and ADFI for week -1. Day 0 BW was included as an additional covariate for day 0 BF and LEA.

Because of the treatment design, the performance traits of BW, ADFI, BF, and LEA while pigs were on treatment were analyzed as repeated measures separately for each treatment, with day 0 BW as a covariate and additional fixed effects of week and the interaction of line and week. For BF and LEA, in addition to day 0 BW, day 0 BF and day 0 LEA were used as covariates, respectively. A first-order autoregressive, AR(1), covariance structure was used to model correlations among pig-specific residuals across time.

The carcass traits of live weight at slaughter, carcass weight, viscera weight, dressing percentage, and chemical carcass composition were analyzed with additional fixed effects of treatment and the interaction of line and treatment, day 0 BW as a covariate, and random effects as previously stated. Litter was removed as a random factor for live weight at slaughter, dressing percentage, and protein percentage because its variance component estimate was not positive for those variables. Slaughter BW was included as an additional covariate for carcass and viscera weight. Because of the large differences in slaughter BW between treatments, this covariate was fitted as the pig's BW minus the average slaughter BW for that treatment, such that least square means were computed for the average BW for each treatment.

For carcass energy, day 0 BW, day 0 BF, and day 0 LEA were included as additional covariates to adjust for differences in carcass energy at the start of the test, such that differences estimated are estimates of differences in retained energy. This analysis assumes that BW, BF and LEA are adequate estimates of carcass energy. This assumption was validated by analyzing carcass energy by the same model but with ultrasound BW, BF, and LEA at slaughter (day 42) as covariates. This model had an R^2 value of 0.92. Gross energy consumed over the 6-week test period was analyzed separately for each treatment with day 0 BW as a covariate.

Maintenance requirements and efficiency of energy retention were estimated by regressing carcass energy on gross energy consumed, following the procedures outlined in Ewan (2001). The carcass energy used in this analysis was adjusted for carcass energy at the start of treatment by adjusting for the effects of day 0 BW, BF, and LEA using regression coefficients obtained from the analysis of carcass energy described previously. Adjusted carcass energy was used as a response variable in a general linear model with fixed effects of line, treatment group, and the interactions of line and treatment group, and covariates of feed energy consumed and its interactions with line and treatment group. Because the linear relationship between energy retained and energy consumed is expected to be consistent for all treatments except for the WS, the Ad, Ad75, and Ad55 treatments were combined into treatment group 1 for this analysis and the WS treatment made up treatment group 2. The interaction of line and treatment group allows separate estimates of maintenance requirements and efficiency for the two treatment groups. To estimate line specific maintenance requirements and efficiency, the interaction of feed energy consumed with line was included in the model. Finally, to test for separate slopes between the two treatment groups, the interaction of feed energy consumed and treatment group was included in the model. The three-way interaction of feed energy consumed with line and treatment group was included in initial analyses but removed because it was not significant.

Results

Performance and Ultrasound

Results for body weight and feed intake data for week -1, along with day 0 BF and LEA, are presented in Table 4.2. Select line pigs consumed 6.7% less feed ($p < 0.06$), with no significant difference in start or end body weight or ADG compared with the Control line. At day 0, Select line pigs had significantly less BF ($p < 0.02$) but similar ($p < 0.41$) LEA. Although day 0 BW did not differ between lines ($p = 0.26$), subsequent results were adjusted by including day 0 BW as a covariate in the models. At day 0, there were no significant differences ($p < 0.75$) in BW, BF, or LEA between the groups of pigs that were randomly assigned to each treatment (results not shown).

Least square means for the repeated measures analysis of BW and ADFI over the six week test period are in Figure 4.1. These data were analyzed separately for each treatment and adjusted for day 0 BW within treatment. As expected, body weight increased incrementally as feed intake increased from treatment WS to Ad. The Ad Select (AdS) pigs consumed less feed than the Ad Control (AdC) pigs (2.6 vs. 2.9 kg/d, $p < 0.09$) over the entire 6 week period. Furthermore, there was no significant difference in BW between the AdS and AdC for any one week. Control Ad75 (C75) and Select Ad75 (S75), and Control Ad55 (C55) and Select Ad55 (S55) pigs consumed the same amount of feed by study design. For Ad75 the two lines had very similar BW throughout the treatment period. For the Ad55 treatment, however, the Select line tended to have greater BW than the Control line and this difference increased as the study progressed. At the end of treatment, the S55 pigs weighed 2.5% more than the C55 pigs ($p = 0.10$).

Despite attempts to keep the WS pigs at a constant BW for six weeks, the main effect of week was highly significant ($p < 0.01$), indicating a change in BW from week 0 to week 6. The Select WS (SWS) pigs weighed 3.5% more ($p = 0.08$) at the end of treatment than the Control WS (CWS) pigs, although their feed intake across the six weeks tended to be lower (7.6%, $p = 0.21$, Figure 4.1). The difference in feed intake between the two lines was significant in weeks 5 (14%, $p < 0.04$) and 6 (18%, $p < 0.02$) (Figure 4.1B). The amount of feed required to maintain BW for the CWS pigs at week 6 did not differ from the requirement calculated at week 1 based on NRC requirements ($p = 0.82$); however, for the SWS pigs, there was a significant decrease in feed intake from week 1 to week 6 (0.82 vs. 0.67 kg, respectively, $p < 0.01$).

The development of BF and LEA, as measured by ultrasound, over the six week period is shown in Figure 4.2. These repeated measures were analyzed separately for each treatment and adjusted for day 0 BW, along with day 0 BF and day 0 LEA for BF and LEA, respectively. On average, BF increased with the amount of feed provided by treatment (Figure 4.2A), although differences not always clearly apparent as C75 pigs had similar BF as the Ad pigs and the S75 pigs had similar BF as the Ad55 pigs. For the Ad treatment, the AdS pigs tended to have less BF than the AdC pigs across the treatment period, although this was non-significant ($p = 0.21$) within any one week. There was no significant difference in LEA development between the AdS and AdC, except on day 28 AdS tended ($p < 0.08$) to have a smaller LEA than the AdC.

Within the Ad75 treatment, the S75 pigs had significantly less BF at days 14, 28, and 42 ($p < 0.01$) and no significant difference in LEA overall ($p = 0.47$), nor any significant differences in LEA within any particular week (Figure 4.2). For the Ad55 treatment, the main effect of week was not significant ($p = 0.30$) for BF but was highly significant ($p < 0.01$) for LEA. For the first 28 days of treatment, the two lines had very similar BF but at day 42 the S55 had 4% more BF than the C55. Although BF did not drastically change, there was a steady divergence in LEA between the two lines under the Ad55 treatment, with the S55 pigs having 3.5% larger LEA at day 42 ($p = 0.23$).

For the WS treatment, the main effect of week was not significant for BF ($p = 0.14$) or LEA ($p = 0.65$) (Figure 4.2). The main effect of line was also not significant for either trait ($p = 0.64$ and $p = 0.33$, respectively), although the SWS had an overall 4% larger LEA. The SWS pigs had a steady loss of BF during treatment, while the CWS pigs initially had a sharp decrease in BF and then a slight increase in BF from week 4 to week 6 (Figure 4.2A). While both lines under the WS treatment had a loss in BF, the CWS also had a slight loss in LEA ($p < 0.90$), while the SWS had a slight increase in LEA ($p = 0.27$).

Melanocortin-4 receptor was non-significant for the majority of the analyses but tended to be significant for day -7 ($p = 0.06$) and -1 BW ($p = 0.08$), and was significant ($p = 0.04$) for week -1 ADFI. For both day -7 and -1 BW, animals homozygous for the 1 allele contained the lowest BW and the heterozygous animals had the heaviest BW. For week -1 ADFI, heterozygotes consumed the most feed and pigs homozygous at the 2 allele consumed the least.

Body and Carcass Composition

The main effect of treatment was highly significant ($p < 0.01$) for all carcass traits, with the exception of dressing percentage (Table 4.3). Least square means for live weight at slaughter were slightly different from the LSM for day 42 BW (Figure 4.1A) because 8 of the 10 replicates were slaughtered, whereas the data for day 42 BW includes all 10 replicates. There was no significant difference between the Select and Control lines in slaughter weight for any treatment after adjusting for day 0 BW. These same results were also found for carcass weight when adjusting for day 0 BW and live BW. However, when averaging over all treatments, there was a significant difference of 0.57 kg carcass weight in favor of the Select line ($p < 0.05$). The Select line also had a 0.62% higher dressing percentage than the Control ($p < 0.03$), again, with no significant difference in carcass weight within treatments. For each treatment, the Select line had lower visceral mass, although this was only significant ($p < 0.02$) for Ad75. Averaging over treatments, the Select line had 0.5 kg lower visceral mass ($p < 0.02$).

The effects of treatment and line on chemical carcass composition are also shown in Table 4.3. Percentages of the main chemical components of carcass protein, lipid, ash, and water added up to 100.1±0.15% of the subsample weight, which confirms the accuracy of the procedures used. The main effect of treatment was significant for water % ($p < 0.01$), protein % ($p < 0.03$), and fat % ($p < 0.01$), with no significant difference between treatments for ash

% ($p < 0.13$). In general, as feed restriction increased the water and protein % increased, and the fat % decreased. Averaged over treatments, there was no significant difference between the lines for any of the chemical carcass composition traits. However, there was a trend for the Select line to have less water, slightly more protein, and less fat than the Control line. For water, fat, and ash %, there were no significant differences between any of the line by treatment combinations. However, when litter was removed from the model with fat % as the response variable, there was a significant ($p < 0.01$) difference between the AdS and AdC pigs. Protein % in the carcass did not differ between the two lines within a given feeding treatment; however, CWS and SWS had significantly more protein % than the AdC.

Carcass Energy

The effects of treatment and line on carcass energy when using the values from calorimetry (BCE) are shown in Table 4.3. The main effect of treatment was highly significant ($p < 0.01$); as expected, greater feed restriction resulted in less carcass energy. The main effect of line was also significant for BCE ($p < 0.04$), indicating that the Select line had less carcass energy relative to the Control; averaged over the treatments, the Select line had 4% less carcass energy. For the analysis of BCE, there was a significant effect of line on carcass energy for the Ad ($p < 0.03$) and 75Ad ($p < 0.02$) treatments, with the Select line having lower carcass energy.

Gross energy consumed was analyzed separately for each treatment; therefore, the main effects of treatment and the interaction of line and treatment were not estimated. No significant differences were found between the Select and Control lines for the Ad and WS treatments. By study design, the Ad75 and Ad55 treatments were to consume the same amount of energy. However, one C75 pig had a reduction in feed intake due to health reasons, causing the Control line to consume slightly less feed. No reductions in growth or other performance measurements were observed on that pig; therefore, that pig was not removed from the analysis.

A scatter plot of adjusted carcass energy vs. energy consumed, including separate regression lines for each line and group, is shown in Figure 4.3. As expected, carcass energy increased with increased energy intake ($R^2 = 0.94$). The difference in the intercepts between the Select and Control lines is an estimate of the difference in maintenance requirements between the two lines. Although the difference (16.5±10.8 Mcal) between the intercepts for the Select and Control lines was not significant ($p < 0.13$), the intercept of the Select line was larger than that of the Control. This suggests that the Select line had a lower maintenance requirement. Additionally, the difference in the slopes between the Select and Control lines is an estimate of the efficiency with which feed energy consumed above maintenance is retained (i.e. a steeper slopes is corresponds to greater energy retention). The 3-way interaction between feed energy consumed, line, and treatment group was dropped from the model due its large p-value (0.88); therefore, the difference of 0.047 in the slope difference between the two lines is the same across the two treatment groups. Although not significant ($p < 0.34$), the Control line had a steeper slope. Within a line, there was a significant difference ($p < 0.05$) in the slopes between the two treatment groups (0.426), with the WS group having a steeper slope.

Discussion

Consistent with results published previously (Cai et al., 2008; Boddicker et al., 2010), the AdS pigs consumed less feed for a similar rate of gain compared to the AdC pigs. Collectively, these findings confirm our hypothesis that, under ad libitum feeding, pigs selected for reduced RFI consume less feed for a given rate of gain. Additionally, the fact that the S55 pigs had a slightly greater gain on the same amount of feed is consistent with our hypothesis that under identically restricted feeding, pigs selected for reduced RFI have a greater rate of gain compared to the Control pigs; however, the fact that the S75 pigs did not have greater gain did not support this hypothesis. Similar results were found in a study that had identical treatments and pigs of a younger age and weight (Boddicker et al., 2010). Furthermore, for the WS treatment, the NRC-based calculation used to determine the initial maintenance energy need was a reasonably accurate estimation for the Control line, as there was essentially no need to change the feed intake from day 0 to day 42 ($p < 0.82$). However, the initial NRC requirements appeared to be high for Select line, as feed intake had to be reduced by nearly 20% from day 0 to day 42 ($p < 0.01$). Interestingly, despite the decrease in feed provided, the Select pigs on the WS treatment continued to increase in BW. This may indicate that the Select line has lower maintenance requirements than the Control line, which will be discussed further later.

Genetic correlations between RFI and BF are generally found to be positive in pigs, ranging from 0.07 to 0.77 (Gilbert et al., 2007; Hoque et al., 2009; Johnson et al., 1999). Although Cai et al. (2008) found a slightly negative genetic correlation between RFI and BF (-0.14) in the lines used in this study, they did find that the select line had less BF than the control line, which would be consistent with a positive genetic correlation. Genetic correlations between RFI and LEA in pigs have generally been found to be negative, ranging from -0.18 to -0.60 (Cai et al., 2008; Hoque et al., 2009; Johnson et al., 1999) and Cai et al. (2008) found that the select line had greater LEA than the control. In this study, the Select line had less BF and more LEA in nearly all treatments, although not always significant (Table 4.3). This is consistent with the line differences observed by Cai et al. (2008) under ad libitum feeding and group housing. These results indicate that the Select line may have a greater lean deposition rate. Boddicker et al. (2010) found that young pigs under WS feeding had more BF and increased LEA. For the WS treatment in the current study, the Select pigs had a similar amount of BF, an increased LEA, and significantly lower feed consumption than the Control pigs, which is consistent to previously reported results, with the exception of FI where no there was no significant difference (Boddicker et al., 2010). This indicates that the Select line is partitioning less of the consumed energy for maintenance requirements than the Control line. These results, however, disagree with the findings from (Cleveland et al., 1983), who found that leaner pigs partition more of their metabolizable energy for maintenance relative to fat pigs. In the current study, the Select line was leaner than the Control, yet required less energy to maintain static BW. This indicates that the Select line does not behave in a manner that is similar to a lean line, but has additional efficiency gains.

Within any one treatment, there were no significant differences in slaughter weight. However, carcass weight tended to be heavier for the Select line which corresponds to a difference in dressing percentage, with the Select line having a 0.62% greater dressing percentage (Table 4.3). Part of the explanation of the increase in dressing percentage is that the Select line had an average 0.36 kg lower visceral mass. This lower visceral mass may also be part of the reason for the increased efficiency of the Select line, as visceral organs have high maintenance requirements. There was a significant treatment effect on visceral mass ($p < 0.01$) which was expected based on the differences between the treatments in the amount of feed provided. However, there was no significant difference in visceral mass ($p < 0.45$) between the Ad75 and Ad treatments. Furthermore, the C75 pigs had the largest visceral mass overall. Although not significant, the Select line had lighter visceral weights than the Control within each treatment. Similar results were found by Wiseman et al. (2007). They found that ad libitum fed pigs that had greater feed intake had larger intestinal tracts and liver weights. Although we did not separate the intestinal tract from the rest of the viscera, our findings suggest that pigs who consume more feed tend to have larger visceral weights. Our data also suggest that pigs selected for lower RFI have lower visceral weights, which was validated by including ADFI as an additional covariate. The Select still had significantly ($p < 0.03$) lower visceral weights compared to the Control.

As the extent of feed restriction increased, water content and protein content of the carcass increased and fat content decreased, indicating an increase in leanness. These same trends were also seen within all treatments between the two lines; overall, there was a trend for the Select line to have less carcass fat content, slightly increased carcass protein content and increased carcass water content, which is consistent with the findings from Boddicker et al. (2010), where pigs were at the beginning of their growth phase, rather than the end. This implies that selecting for lower RFI has increased carcass leanness.

In beef cattle, steer progeny of low and high RFI parents had similar differences in carcass characteristics as the current study found; progeny from low RFI parents had less BF and more protein than progeny from high RFI parents (Richardson et al., 2001). These differences in steer progeny chemical carcass composition, however, accounted for only 5%

of the difference in RFI (Richardson et al., 2001). In young pigs, Boddicker et al. (2010) estimated that, under ad libitum feeding, the difference in carcass composition between a low RFI and control line may explain 87% of the difference in feed intake. To evaluate the extent to which differences in feed intake could be explained by differences in carcass composition in our study, net energy consumed was estimated to be 56% of gross energy consumed (Oresanya et al., 2008), using the LSM of Table 4.3. Then, line differences in net energy consumed were compared to estimated line differences in carcass energy retained, using LSM of Table 4.3. For the Ad treatment, the line difference in net energy consumed was (487.1 - 464.3)*0.56 = 12.8 Mcal, whereas the line difference in retained energy was 322.0-302.8 = 19.2. Similar results, i.e. that the difference in retained carcass energy were greater than the estimated differences in net energy consumed, were observed for the other three treatments. Assuming that the assumptions that underlie these calculations are correct, this suggests that the difference in feed intake between the two lines may be partially explained by the differences in carcass composition. The difference in carcass composition was primarily caused by differences in fat content between the two lines. The AdC pigs consumed more energy and had greater carcass fat. The C75 pigs appear to be more efficient at retaining the energy consumed by storing it as fat. The S55 pigs had slightly greater carcass energy, but again, this may be due to the greater increase in body weight, and as seen from chemical carcass composition, the C55 pigs had greater chemical carcass fat. If there was no significant difference in final BW, the Control line may have had greater carcass energy.

Maintenance energy requirements are believed to be associated with RFI. Selection for lower RFI resulted in lower maintenance requirements in beef cattle (Herd and Bishop, 2000). Based on regression analysis presented in Figure 4.3, the Select line appears to have lower maintenance requirements than to the Control, which is noted by the Select line having a higher intercept. Lower maintenance requirements of the Select line are also indicated by it requiring substantially less feed to maintain constant body weight under the weight stasis treatment and by the Select line having lower viscera mass. However, as previously discussed, most, if not all, of the differences in feed intake between the two lines were accounted for by the difference in carcass energy between the Select and Control lines. In addition, the slopes of the regression lines in Figure 4.3, which are estimates of the efficiency of retaining the energy consumed, suggest that the Control line, by having a steeper slope, may in fact be more efficient in converting feed energy above maintenance into retained energy. However, it appears that the Control line is retaining the extra energy they consume as fat rather than lean, which is not necessarily desirable from a production stand point. This is further supported by findings from Boddicker et al. (2010) who found no significant differences in the slopes between low RFI and control pigs at a young age. This supports the current findings because the variation in BF increases with an increase in BW, explaining the steeper slope of the Control line as they have more BF than the Select line. Further work is needed to investigate the somewhat contradictory results that were obtained in this study on the importance of maintenance requirements, carcass composition, and energy retention for the difference between the Select and Control lines; results obtained herein must be viewed with caution as the sample size was small. Nevertheless, results do show that selection for low RFI in Yorkshire pigs has reduced feed intake by approximately 9% on ad libitum feeding at no expense to carcass yield or growth rates and a greater lean percentage, which increases profitability to the producer. Under restricted feeding in the Select line had slightly heavier carcass weights than the Control line, indicating that the low RFI line is more efficient in partitioning, not retaining, the energy consumed. Furthermore, carcass composition and maintenance energy requirements are the main biological factors that contribute to RFI in pigs.

Implications

The results of this study show that selection for low RFI does indeed improve feed efficiency, with little differences in growth. In addition, this study indicates that selection also changes carcass composition, yet the overall carcass composition may explain most, if not all, of the difference in feed intake. RFI may be another important measure of feed efficiency that is more accurate than the feed conversion ratios that have been historically used as the basis for genetic selection to improve feed efficiency.

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Table 4.1. Diet Composition

Ingredient	%
Corn, Grain	74.38
Soybean Meal-48	16.91
Soybean Hulls	5.00
Soybean Oil	1.00
Limestone	0.91
Monobasic Calcium Phosphate	0.73
Vitamin Mix[1]	0.50
Salt	0.35
Mineral Mix[2]	0.10
L-Lysine HCl	0.07
Selenium	0.05
Calculated analysis, %	
Crude Protein	15.25
Lysine	0.75
Calcium	0.45
Available Phosphorus	0.25
Metabolizable energy, Kcal/g	3265.00

[1] Vitamin mix donated by DSM Nutritional Products, Inc., Ames IA 50010 and provided the following per kilogram of diet: vitamin A, 4,409 IU; vitamin E, 22 IU; vitamin D3, 1,102; niacin, 33mg, D-pantothenic acid, 18 mg; riboflavin, 6.6 mg.

[2] Mineral mix provided the following per kilogram of diet: Zn, 90 mg as ZnO; Fe_2SO_4; Cu, 10.5 mg as CuO; Mn, 36 mg as MnO_2; I, 1.2 mg as CaI.

Table 4.2. Effects of selection on body weight and feed intake of pigs from the selected or control line. Start and end of the week prior to dietary treatment, along with ultrasonic backfat and loin eye area at the start of treatment. Data represents least square means ± SEM, n = 40 pigs per line.

Item	Select line	Control line	p-value
Day -7 to Day -1			
Start weight, kg	68.4 ± 1.5	68.9 ± 1.6	0.81
End weight, kg[1]	76.2 ± 0.28	75.9 ± 0.29	0.53
Feed intake, kg/d	2.36 ± 0.06	2.53 ± 0.06	0.06
Daily gain, g/d	890.2 ± 38.3	863.3 ± 38.9	0.60
On-test (Day 0)			
Body weight, kg[1]	73.7±1.6	75.4±1.7	0.26
Backfat, mm	15.6 ± 0.50	17.4 ± 0.54	0.02
Loin eye area, cm^2	32.4 ± 0.65	31.8 ± 0.69	0.41

[1] Body weights differ due to an overnight fast from day -1 to day 0.

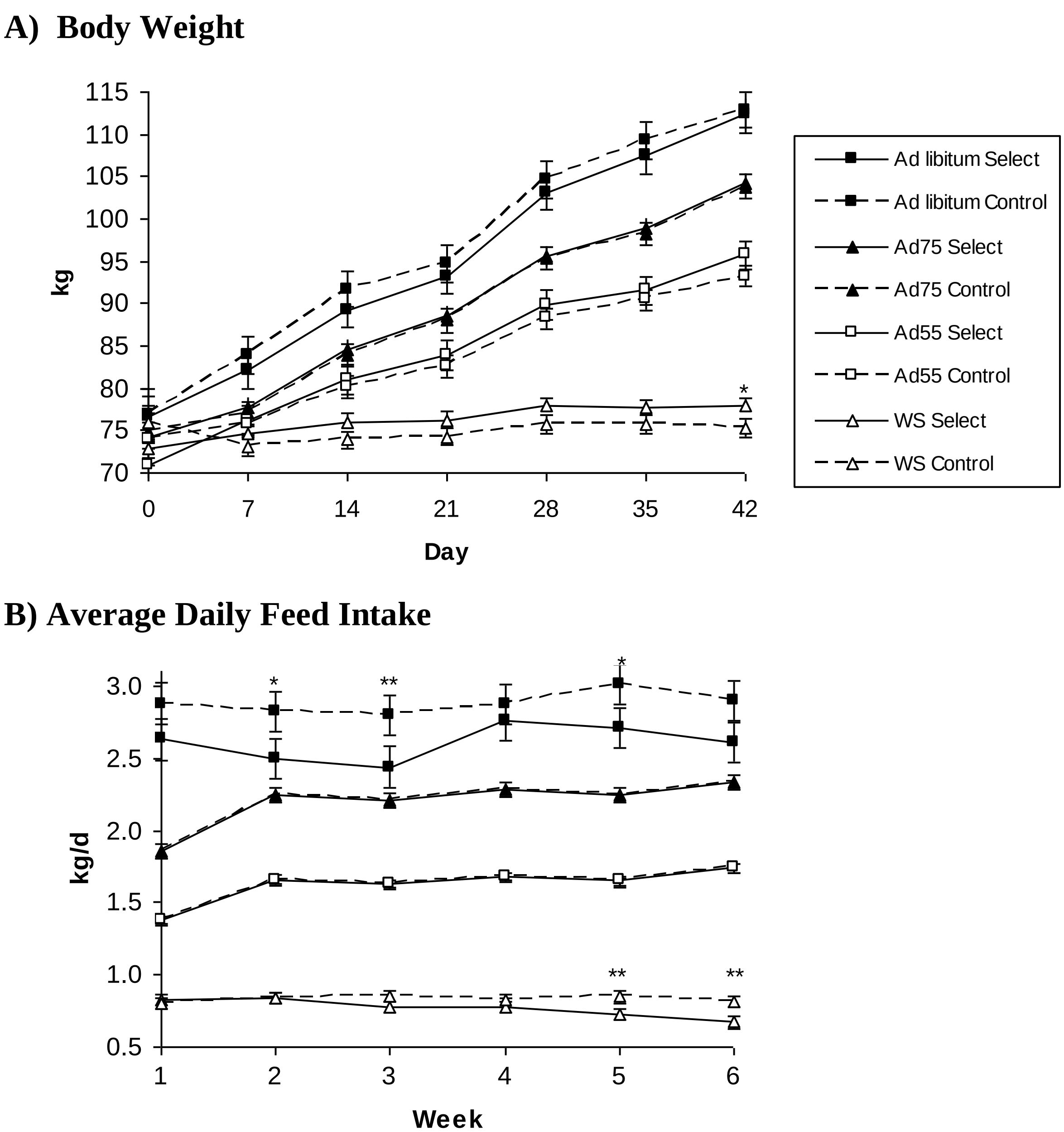
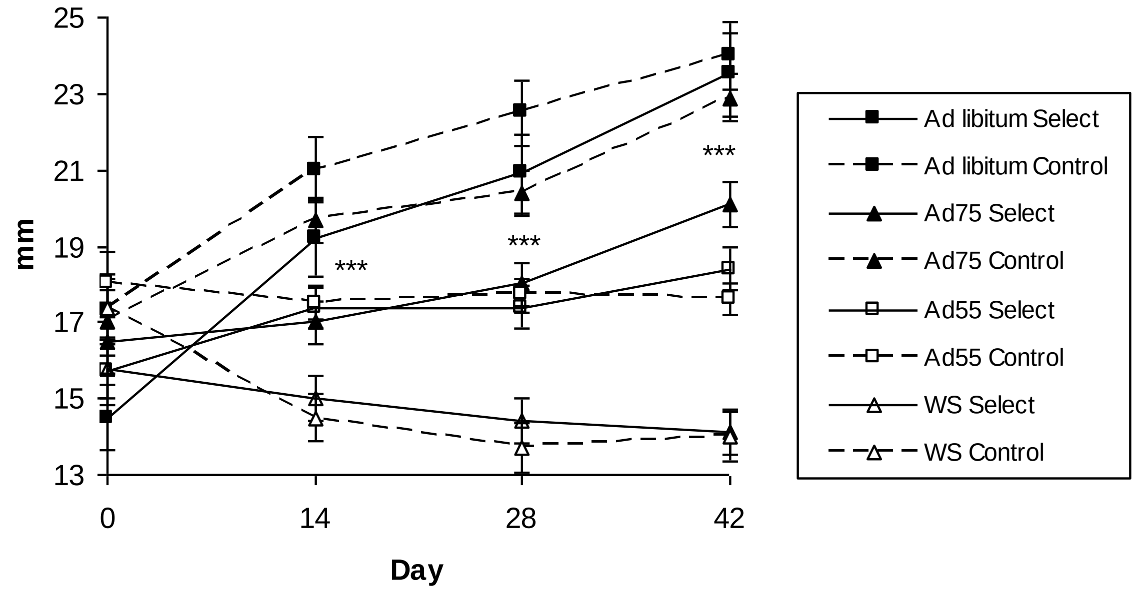


Figure 4.1. Effects of diet restriction on body weight (A) and average daily feed intake (B) of control and low residual feed intake finisher barrows. Panel A represents body weight every 7 days (least square means ± SEM), n is 10 per line per treatment. Panel B represents weekly average daily feed intake (least square means ± SEM), n is 10 per line per treatment.

A) Backfat



B) Loin Eye Area

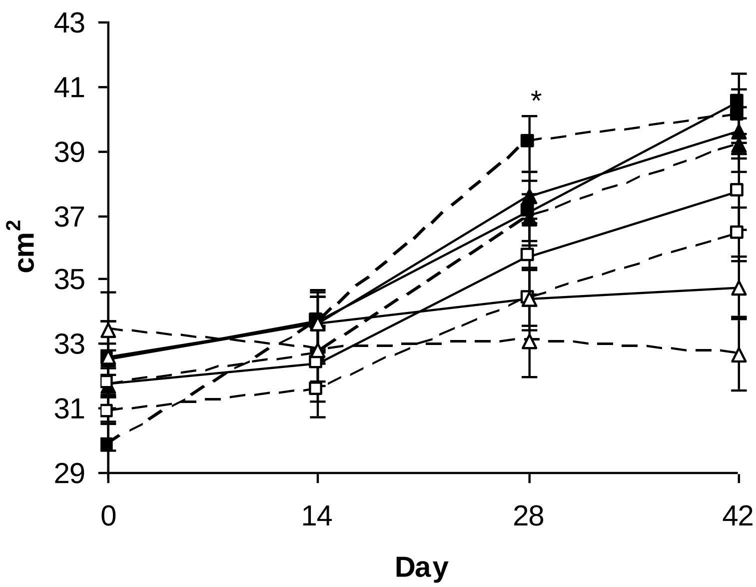


Figure 4.2. Effects of diet restriction on BF (A) and LEA (B) of control and low residual feed intake finisher barrows. Panel A represents BF every 2 weeks (least square means ± SEM), n is 10 per line per treatment. Panel B represents LEA every 2 weeks (least square means ± SEM), n is 10 per line per treatment.

Table 4.3. Least square means of treatment (T) and line (L) on body and carcass composition for the eight pigs per line and treatment that were harvested[1]

Carcass	Genetic Line and Treatment									p –value		
Carcass	Ad libitum		75% of Ad libitum		55% of Ad libitum		Weight Stasis		Line			
Item	Select	Control	Select	Control	Select	Control	Select	Control	difference[2]	L	T	L*T[3]
Live weight, kg[7]	114.6±1.3[d]	115.2±1.3[d]	106.0±1.3[c]	108.2±1.2[c]	97.3±1.3[b]	97.8±1.3[b]	77.5±1.3[a]	78.4±1.3[a]	1.03±0.88	0.25	0.01	0.89
Day 42 BF, mm[9]	23.3±0.67[de]	24.8±0.63[e]	20.3±0.61[c]	22.6±0.61[d]	17.9±0.65[b]	17.7±0.64[b]	14.2±0.62[a]	14.7±0.63[a]	0.10±0.04	0.03	0.01	0.16
Day 42 LEA, sq. cm[10]	41.2±0.86[d]	40.2±0.85[cd]	39.3±0.80[bcd]	39.1±0.80[bcd]	38.4±0.86[bc]	37.6±0.83[b]	32.8±0.80[a]	31.3±0.84[a]	-0.88±0.55	0.12	0.01	0.84
Carcass weight, kg[4, 8]	98.0±0.41[d]	97.3±0.41[d]	90.3±0.41[c]	89.6±0.40[c]	82.7±0.43[b]	82.2±0.40[b]	66.3±0.41[a]	65.8±0.41[a]	-0.57±0.29	0.07	0.01	0.99
Dressing %[6, 7]	85.3±0.39[b]	84.8±0.39[ab]	84.4±0.39[ab]	83.7±0.38[a]	84.8±0.42[ab]	84.2±0.39[ab]	85.1±0.41[b]	84.5±0.40[ab]	-0.62±0.62	0.03	0.11	0.99
Viscera, kg[5, 8]	13.8±0.32[c]	14.2±0.30[cd]	13.8±0.32[c]	14.5±0.30[d]	12.4±0.31[b]	12.7±0.30[b]	9.9±0.30[a]	10.0±0.30[a]	0.36±0.17	0.05	0.01	0.46
Chemical Composition, % of Carcass												
Water, %[7]	55.3±1.1	51.2±1.0	54.6±0.98	53.8±1.0	57.4±1.1	55.1±1.0	60.7±1.0	59.1±1.0	-2.18±0.64	0.18	0.01	0.56
Protein, %[7]	17.6±0.57[ab]	17.2±0.56[a]	17.5±0.52[ab]	17.8±0.54[abc]	18.7±0.58[abc]	17.5±0.55[ab]	18.8±0.54[bc]	19.3±0.54[bc]	-0.20±0.38	0.60	0.03	0.40
Fat, %[7]	24.1±1.4	29.6±1.4	25.6±1.3	25.9±1.4	21.6±1.5	24.7±1.4	16.8±1.4	18.9±1.4	2.72±0.95	0.21	0.01	0.53
Ash, %[7]	2.9±0.13	2.7±0.13	2.9±0.12	2.7±0.12	2.9±0.13	2.7±0.12	3.1±0.13	3.0±0.12	-0.15±0.10	0.37	0.13	0.95
Carcass Energy, Mcal/pig												
CE[11]	302.8±7.0[e]	322.0±7.0[f]	263.0±6.7[c]	282.2±6.7[d]	232.6±6.9[b]	231.4±6.9[b]	163.3±6.8[a]	164.2±6.9[a]	9.50±4.2	0.04	0.01	0.13
GEC[12]	464.3±18.4	487.1±18.4	360.3±3.3	356.0±3.3	264.4±0.0	264.4±0.0	141.1±1.9	142.4±1.9	--	--	--	--

[a,b,c,d,e,f] Different letters in a row represent significant differences at $p < 0.05$
[1] Values are least square means based on 8 pigs per line per treatment
[2] Difference of control minus select
[3] Interaction of line by treatment
[4] Carcass equals empty body weight, including head and hair
[5] Viscera includes entire intestinal tract with contents, kidney, heart, and lungs
[6] Dressing percentage is carcass weight as a percent of slaughter weight
[7] Analysis included week 0 body weight as a covariate
[8] Analysis included week 0 body weight and adjusted slaughter weight (average slaughter body weight within each treatment minus individual pig's slaughter body weight) as covariates
[9] Analysis included day 0 body weight and day 0 backfat
[10] Analysis included day 0 body weight and day 0 loin eye area
[11] Carcass energy determined from adiabatic bomb calorimetry
[12] Gross energy consumed over the 6 week test period (analyzed per treatment)

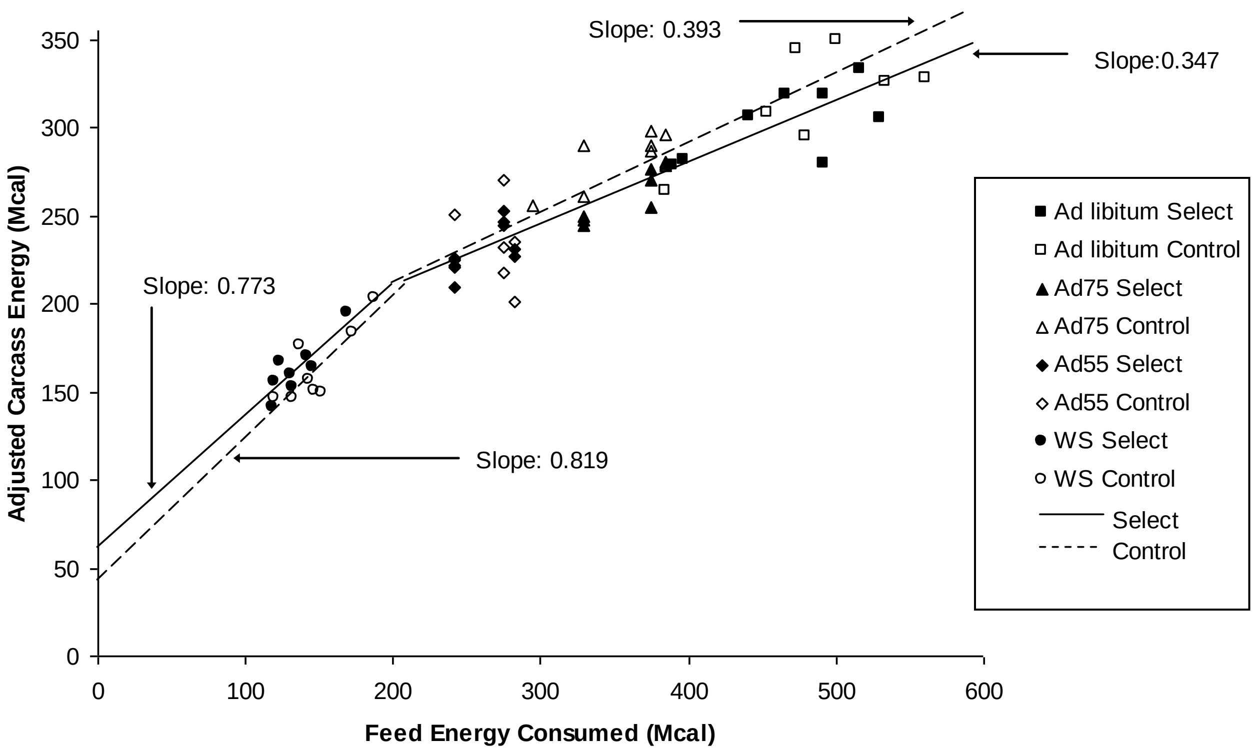


Figure 4.3. Carcass energy, adjusted for initial carcass energy, against total feed energy consumed over the six week test period.

CHAPTER 5. GENERAL DISCUSSION

Feed efficiency and residual feed intake as a unique measure of feed efficiency

Feed efficiency is an important production and economic trait in livestock production. However, the physiological basis for improved feed efficiency in animal agriculture is poorly understood. Residual feed intake (RFI) is a unique measure of feed efficiency as it is adjusted for the production traits of growth and backfat, i.e. it represents feed intake given an amount of growth and backfat. In contrast, traditional measures of feed efficiency such as feed:gain and gain:feed ratios are associated with growth and backfat. Therefore, selection for reduced RFI is appealing to producers as they reduce their cost of feed without compromising days to market. The Yorkshire pig RFI selection lines at Iowa State University are a unique population to study because they provide a platform to understand not only response to genetic selection, but to understand the biological mechanisms that control response to selection and that determine differences in feed efficiency.

With the identification of the biological mechanisms contributing to the variation associated with RFI, feasible methods to select for reduced RFI can be developed. In beef cattle, protein turnover, tissue metabolism, and stress (37%), digestibility (10%), physical activity (10%), feeding behavior (2%), heat increment of fermentation (9%), and body composition (5%) have been identified as the main biological factors that contribute up to 73% of the variation in RFI, with the remaining 27% classified as “other” mechanisms (Richardson and Herd, 2004a). Maintenance energy requirements have been found to be positively correlated with RFI in beef cattle (Castro Bulle et al., 2007; Herd and Bishop, 2000) and chicken (Luiting et al., 1991; Van Eerden et al., 2006) and may account for a portion of the “other” category. This thesis examined the contribution of carcass composition and predicted maintenance energy requirements towards the differences between the Iowa State University pig RFI lines and to determine the critical points of the growth curve when the low RFI line and randomly selected control line diverge in carcass composition, maintenance requirements, and performance traits such as feed intake and growth.

Pig Performance

Residual feed intake is reported to be positively correlated to the performance trait of feed intake (Cai et al., 2008; Gilbert et al., 2007; Hoque et al., 2009). Furthermore, Cai et al. (2008) found that pigs selected for low residual feed intake consumed less feed compared to a randomly selected control line in group housing. Consistent with these findings, under ad libitum (Ad) feeding in early (EGP) (Chapter 3) and late stages (LGP) (Chapter 4) of the growth curve and individual pens, low residual feed intake (Select) pigs consumed less feed than the randomly selected control (Control) pigs. Cai et al. (2010) reported that after 5 generations of selection for reduced RFI, the low RFI line and randomly selected control line did not diverge in daily feed intake until the end of the growth period. However, in the work described here, divergence in feed intake was apparent in the early phase of the growth curve (Chapter 3), indicating that the divergence in feed consumption begins to form at a relatively young age. In the studies presented here, pigs were individually penned, whereas results form Cai et al. (2010) were from group housing, where there is potential competition for food, which could partially explain this difference in results. Nonetheless, there is a difference in feed intake between pigs selected for reduced residual feed intake and randomly selected control pigs, but little is known about the physiological mechanisms that drive this divergence in feed intake. One explanation may be differences in appetite regulation, which is controlled partially by melanocortin-4 receptor (Kim et al., 2000), leptin concentrations, and the hypothalamus. Furthermore, there was no significant difference in body weight between the two lines within either the EGP or LGP (Chapters 3 and 4, respectively). These results also contradict the previous work in the ISU population reported by Cai et al. (2010) where the low RFI pigs began to diverge in body weight, at approximately 70 kg, from a randomly selected control line. Again, these differences may be attributed to differences in pen settings (individual vs. group) and in social or feeding behavior.

Collectively, under Ad feeding, the Select line had increased feed efficiency, as they consumed less feed without detrimental effects on growth. These results are the backbone of the hypothesis that, under identically restricted feed intake between the Select and Control line, the Select line will have increased growth compared to the Control. We found that the Select and Control pigs fed identically restricted rations resulted in a significant increase in body weight in the Select line under 75% of Ad feed (Ad75) in EGP (Chapter 3) and 55% of Ad feed (Ad55) in LGP (Chapter 4) compared to their Control counterparts. These results support our hypothesis and the increased feed efficiency found in the Select Ad libitum pigs.

In beef cattle, feeding patterns are estimated to explain 2% of the variation associated with RFI, as determined from experiments on divergently selected beef cattle (Richardson and Herd, 2004a). In swine, however, many feeding behavior traits, such as feeder visits per day and eating rate, were not found to be associated with RFI (Rauw et al., 2006; Von Felde et al., 1996). In the current experiments, pigs were individually penned and were given different rations. Feeding behavior traits were not quantified in pigs on the Ad treatment, while pigs on restricted and weight stasis feeding were fed twice per day and consumed the rationed feed immediately. Although not part of this thesis, litter mates to the pigs used in Chapters 3 and 4 have been assessed for feeding behavior trait differences (Young et al., 2009). The key feeding behavior traits of feed intake per visit and number of visits per day were not significantly different between the low RFI and the randomly selected control line; however, feeding rate per visit was higher in the low RFI. Although the variation in RFI due to feeding behavior has not been quantified in pigs, it appears that feeding behavior has a minimal contribution in explaining the biological variation associated with RFI.

In beef cattle, physical activity explains 10% of the variation in RFI. In the current studies, the Select line consumed less feed compared to the control line under the Ad treatment, even though the pigs were individually penned. Here, physical activity was restricted and can be assumed to be the same between lines. Therefore, physical activity appears to contribute little to no variation in RFI in the studies described in this thesis. However, pigs individually penned will perform better than pigs in group housing due to different environments, which include competition and aggressive behavior towards other pigs. Therefore, physical activity cannot be ruled out as a contributor to the differences observed in RFI.

Carcass Composition and Ultrasound growth data

In beef cattle, proximate analysis of body chemical composition, as measured by protein, fat, and ash content, accounts for only 5% of the difference in RFI (Richardson et al., 2001). Carcass composition is correlated with genetic variation in RFI, with low RFI steers having lower whole body chemical fat and higher body protein that steers from high RFI breeding (Richardson et al., 2001). Similar to beef cattle, the genetic correlation between RFI and backfat, which is an indicator of carcass composition on the live animal, has generally been found to be positive in pigs, ranging from 0.07 to 0.77 (Gilbert et al., 2007; Hoque et al., 2009; Johnson et al., 1999). Conversely, the genetic correlation between RFI and loin eye area is generally found to be negative in pigs, ranging from -0.18 to -0.60 (Cai et al., 2008; Hoque et al., 2009; Johnson et al., 1999). Therefore, selection for reduced RFI results in leaner pigs compared to pigs with high RFI, which is favorable as lean tissue is less expensive to deposit compared to fat tissue (Tess et al., 1984). In the current experiments, the Select line had significantly less carcass energy, as determined by adiabatic bomb calorimetry, within the Ad treatment for EGP (Chapter 3) and within the Ad and Ad75 treatments for LGP (Chapter 4). This difference in carcass energy is primarily explained by the fact that the Control line had more carcass fat compared to the Select line within the Ad treatment for EGP, more backfat and carcass fat within the Ad treatment for LGP, and increased backfat within the Ad75 treatment for LGP. This increase in backfat and carcass fat leads to increased carcass energy because fat has more energy per gram than protein (Ewan, 2001). Given certain assumptions, this difference in chemical carcass composition accounted for 87% (Chapter 3) to over 100% (Chapter 4) of the difference in feed intake between the Select and Control lines under ad libitum feeding for EGP and LGP. Although these results are estimates and must be interpreted with caution, it appears that chemical carcass composition may explain a large proportion of the difference in RFI in pigs, even to a greater extent than in beef cattle.

Using linear regression we found that, as a whole, the Control line was more efficient in retaining the energy consumed for LGP. However, there appeared to be a difference in the partitioning of the energy consumed between the two lines, which can be supported by the increase in carcass fat% and increased backfat found in the control line. Therefore, the Select line deposited more lean content than the control, which is also supported by the fact that loin eye area was significantly larger in the Select line for the Ad75 treatment, compared to the control for EGP (Chapter 3) and a trend for the Select line to have a larger loin eye area for LGP. Despite the fact that the Control line retained more consumed energy as a whole, the Select line is more feed efficient because of the increased efficiency for lean deposition. Furthermore, the difference in energy partitioning was apparent in the weight stasis treatment, as the Select and Control lines both lost backfat under severe feed restriction; however, the Select line lost less backfat than the Control for EGP (Chapter 3) and LGP (Chapter 4). These results are only estimates of energy retention and must be interpreted with caution, as no pigs were slaughtered at the beginning of either experiment, which is required to truly calculate retained energy throughout the test period. Therefore, further research is required to calculate actual retained energy and feed intake data to determine the true proportion of carcass composition that contributes to the difference in residual feed intake.

In general, there were no significant differences in slaughter weights between the Select and Control lines within treatments and experiments. However, dressing percentage was greater in the Select line compared to the control for LGP (Chapter 4), but not for EGP (Chapter 3). The results from LGP support the findings from (Gilbert et al., 2007), who found a negative genetic correlation (r = -0.36) between RFI and dressing percentage of pigs slaughtered at market weight (107 kg). This increase in dressing percentage of the Select line may be explained by the lighter visceral weights of the Select line at market age. Furthermore, the lower visceral weights in the Select line may directly relate to reduced maintenance requirements.

Maintenance

Reduced RFI has been reported to be associated with lower maintenance requirements. Selection for reduced RFI in beef cattle resulted in lower maintenance requirements, estimated by the difference between total metabolizable energy intake and metabolizable energy required for growth, as the two traits had high phenotypic and genetic correlations (Herd and Bishop, 2000). These high correlations imply that maintenance requirements play a substantial role in the variation of RFI. Furthermore, laying hens with lower RFI had lower basal metabolic rate and produced less body heat than hens with high RFI (Luiting et al., 1991). Van Eerden et al. (2006) reported that pullets with high RFI put more total energy into maintenance. In order to test whether maintenance requirements differed between the low and control RFI pig lines, we designed a graded feeding experiment (weight stasis, Ad55, Ad75 and Ad). We hypothesized that, under weight stasis feeding, the Select line would require less feed to maintain static body weight and found that the Select line required an overall 8% less feed to maintain static body weight, with an 18% difference at the end of the test period for LGP, but not for EGP. The fact that the Select line under the weight stasis treatment required significantly less feed to maintain body weight indicates that selection for reduced RFI results in reduced maintenance requirements. Additionally, using regression of consumed on estimated retained energy, maintenance requirements were found to be reduced in the Select line, compared to the Control line, for LGP (Chapter 4), but not for EGP (Chapter 3). However, these are only estimates and must be interpreted with caution. True measurements of maintenance energy requirements need to be determined to estimate the proportion of maintenance requirements and its contribution to the differences in RFI. However, measuring maintenance requirements is laborious and expensive, as it typically requires respiratory chambers to directly measure total heat loss. Nonetheless, one explanation for the reduced maintenance requirements in low RFI pigs is fact that the Select line had lower visceral weights (Chapter 4). Noblet et al. (1999) estimated that visceral mass contributed 3 times more energy (kJ/kg-viscera$^{.70}$) towards maintenance than did muscle mass. Because viscera, compared to skeletal muscle, is energy expensive to maintain (Noblet et al., 1999), a reduction in visceral mass results in less energy partitioned to viscera and increased feed efficiency. Furthermore, this difference may be due to different costs in energy expenditure to transport Na^{+}/K^{+} and Ca^{2+} across the cell membrane between the Select and Control lines (Gill et al., 1989; Milligan and McBride, 1985).

Digestibility explained 10% of the variation in RFI in beef cattle (Richardson and Herd, 2004a). Conversely, differences in digestibility in poultry (Luiting et al., 1994) and pigs (de Haer et al., 1993) did not contribute to the variation in RFI. This difference between monogastrics and ruminants may largely be due to differences in digestive systems. Therefore, 10% of the variation in RFI due to digestibility is captured elsewhere in pigs. This 10% in beef cattle may be partitioned in carcass composition, as we found carcass composition plays a significant role in the variation in RFI, whereas Richardson and Herd (2004a) reported that only 5% of the of the variation in RFI is explained by carcass composition.

In beef cattle, Richardson and Herd (2001) reported the main biological factors that contributed to differences in RFI and graphically represented them in a pie chart. Redefining the pie chart for swine, chemical carcass composition contributed a large proportion of the variation in RFI (greater than 80%), with maintenance requirements contributing a smaller proportion to the variation in RFI, compared to chemical carcass composition. Therefore, the main biological factor of body composition that contributes to differences in RFI in swine has a very different proportion than what was found in beef cattle.

Implications

Results from the current experiments provide the base information on some of the main biological factors that contribute to differences in RFI, such as carcass composition and maintenance requirements. Chemical carcass composition appears to account for a large proportion of the differences in RFI and is primarily driven by the difference in backfat and carcass fat percent. Nonetheless, RFI does improve feed efficiency and further research is required to obtain a greater understanding of the biological mechanisms that contribute to the variation in RFI. Ultimately, this will aid in animal selection criteria to improve production efficiency and breeding and management programs.

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